THE ANALYSIS OF CHARACTERS IN CORN AND THEIR BEHAVIOR IN TRANSMISSION

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BY

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INTRODUCTION.

The work, of which this paper is a partial report, has in reality been a search for characters in the corn plant; how many and what are they; how do they behave in transmission? In the general plan of the investigation, it was decided to begin with the germinating seed and continue through the life history of the plant, going as far as time and facilities would permit.* The plan followed was to study *characters* wherever they might be found, rather than to make a group study of varieties or strains as a whole. The topics used as headings in the report of the investigation are not necessarily characters of last analysis, but may represent more or less complex bundles of genetic units.

To a very large extent, investigators in hybridization, before Mendel's law was applied, saw their material in generalities. Mendel's far-sightedness in comparing *individual characters* only and not plants as a whole, together with his careful watch upon the behavior of these individual characters through several generations of the progeny, enabled him to secure the facts which led to the discovery of this great law, overwhelming in its importance, which bears his name. Following its rediscovery in 1900, methods in the study of heredity have been revolutionized. Thus the era of mass selection in corn breeding is also rapidly passing and the practice is to be superseded by more rational methods.

Some general principles of heredity, which have a direct bearing on the subject in hand, will be considered briefly before entering into the discussion of the characters themselves.

VARIATION AND SELECTION.

In a wind-pollenated plant like corn, we must expect great diversity unless the parents have been inbred for a number of generations. In ordinary seed corn, then, we have the opposite to what Johannsen has called a "pure line". "A pure line may be defined as the descendants from one single homozygotic organism, exclusively propogating by self-fertilization. 'Pure line' is merely a genealogical term, indicating nothing as to the qualities of the individuals in question. A 'line' ceases to be pure when hybridization (or even intercrossing) disturbs the continuity of self-fertilization."46)

We cannot conceive of variation being a haphazard phenomenon, but rather that it is governed by definite laws. In such a study as this, the question naturally arises as to the methods and causes of variations observed and the possibility of controlling them. Anything gained in this direction, adds to our knowledge of what we are dealing with in the selection of variations already existing.

Since we have a mixed ancestry in corn, there is much significance in the suggestion,—that, in general, gains secured in selection in corn are not fluctuations inherited, but rather the products from a mixture of types long existing and which selection partially segregates.

Considerable confusion exists in literature in regard to the word "selection". It is improbable that any thoughtful writer claims that the act of selection itself—of either mutations or fluctuations—produces any genetic change in an organism, since

*The tabulation of the *plant* characters consumed so much time that the writer was unable, in the time allotted, to compile and report the data secured on the *ear* and *kernel* characters.

In order to save expense in publishing, the original thesis has also been considerably abbreviated by the removal of the voluminous tabular matter and the discussion relating to it. This paper, therefore, contains only a general discussion of some of the *plant* or "vegetative" characters studied in the investigation, of which this is only a partial report.

the differences, which we see expressed in the soma or body, existed before the selection was made, otherwise there would be nothing to select. The question to be decided finally is not; whether "selection" produces anything new; but, are small variations (so-called "continuous fluctuations") inherited? Are small variations due to differences in environment and food only? May they not be of greater significance in total differentiation than a limited number of mutations ("discontinuous fluctuations") in the evolution of a race? Selection is the tool, not the cause.

One writer has the following to say about selection: "Within pure lines, if no mutations or other disturbances have been at work, or within a population in which there is no genotypical difference, selection will have no hereditary influence." This must be granted at once, since the clause "mutation or other disturbances" excludes everything else. Neither is there anything left to work on if we allow the term "small mutations", which is used by some writers to explain the results gained by the use of fluctuations, granting that fluctuations are cumulative.

ENVIRONMENTAL INFLUENCES.

It has long been known that corn is very responsive to environment and in order to get normal development, which the farmer calls "best results", the seed should come from the region in which the crop is grown. Tests at the various experiment stations have substantiated this principle. In investigations, such as the present one, it is evident that environmental influences must be carefully considered in the interpretation of results and especially upon corn which has not come from "home grown" seed.

A number of varieties used in my study were imported from other states, Mexico, and Central America. The behavior of these varieties including widely different habits of growth, enabled me to compare adaptations to the environment here in Illinois. Some of the varieties produced few or no viable seeds, because of the short season to which they were poorly adapted. In some cases, pollen only was secured and this was applied to silks of earlier maturing varieties. It may be that this is the most successful way (hybridization) in which desirable characters of varieties requiring a long growing season may be introduced into a region having a short season. Collins 18) reported that first generation hybrids are relatively free from the new place effects.

ABNORMALITIES.

Many abnormalities were found in this work, some of which are of particular interest and which will be mentioned in connection with the characters to which they are related. Blaringhem 9) described several new races which came from mutilated plants of an eight-rowed yellow flint variety. He reports obtaining a constant hermaphrodite form, another with white grains, and other differences in plant structure. He states that abnormalities were much more constant in the progeny of the mutilated plants than when found in plants not mutilated. Why this should be, he does not explain, except in the cases that were close—or self—fertilized. Sturtevant 80) mentioned a number of similar obnormalities, some being secured by mutilation, but of which none were reproduced in one trial with open pollenated seed. We have found all the abnormalities mentioned by Blaringhem and Sturtevant, and many others during the two seasons in which our work was in progress, and none of them, so far as known, were due to mechanical mutilations. It is possible that the white strain which Blaringhem secured, may be the result of segregation from the yellow variety as Shull has secured a yellow strain from a mixed white variety by self-breeding. The corn plant undoubtedly furnishes a rich field for investigation in the above mentioned class of study.

In varieties that are thoroughly acclimated, the question of vigor is an important factor, and one which may obscure the development of certain characters in both pure and hybrid plants. One of the objects of the study was to get additional information upon this much discussed topic. Vigor in corn has been investigated from two standpoints; wide-bred, and inbred populations.

The question was perhaps first studied from the wide-bred standpoint by W. J. Beal 6), who concluded as follows: "To improve or infuse new vigor into varieties—plant near each other and mix them—good results of such crossing will last for several years, though most apparent the first year." Other experiment stations were asked to take part in this investigation, but the reports were generally indefinite. Beal's own results with yield tests were very satisfactory, as is shown by the following proportionate yields which he obtained:

	"From Crossed Seed."	"Seed Not Crossed."
1878........................	109.67	100
1881........................	121	100

So far as known, Beal's method of securing hybrid seed is the first reported instance in which detasseling was put to any extensive use. This method was used later by Burrill, Sturtevant, and others, and was finally adopted as a practical method to prevent inbreeding.

Results by McCluer and Morrow and Gardner a decade later confirmed the work of Professor Beal. McCluer 57) found that "The corn grown from the crossed seed was in nearly all cases clearly increased in size [ears larger than those of either parent] as a result of crossing—nearly all the corn grown a second year from the crosses is smaller than that grown the first year, though most of it is yet larger than the average size of the parent varieties." Morrow and Gardner 62) noted that "In every instance the yield from the cross is greater than the average from the parent varieties; the average increase per acre from the five crosses being 9.5 bushels."* But this conclusion does not give the most important part of the results as may be seen by a rearrangement of their data.

Yields in bushels of air dry corn per acre:

No.	Parent yields.	Average of parents.	Yield of Hybrid.	Increase over average of of parents.	Increase over higher-yielding parent.
1.	A-64.2 B-61.6...........	62.9	64.1	1.2	—.1
2.	A-64.2 C-79.2...........	71.7	73.1	1.4	—6.1
3.	D-73.6 E-65.1...........	69.3	86.2	16.9	12.6
4.	F-60.6 D-73.6...........	67.1	76.2	9.1	2.6
5.	A-64.2 G-58.4...........	61.3	78.5	17.2	14.3
	Averages................	66.5	75.6	9.2	5.9

Evidently nothing would be gained by making such hybrids as No's 1 and 2, while such hybrids as No's 3 and 5 would be very profitable because the yields were, in each case, much higher than that of either parent. What might have been secured from other combinations of these same parents could be told only by trial. Some of the other possible combinations might have given greater yields than either of those tried, since there is evidence that some of the hybrids were more favorable combinations than others. Reports of a later, similiar test by the same authors 63) show somewhat less gains from hybridization than in the first report. The system of checking field results, used by these early workers, was imperfect and consequently the yields reported are not absolutely reliable.

Hartley 42) states that "in some instances, cross bred seed produces less than the average of the strains crossed." Collins 16) found similiar cases and recommends that "we should lose no time in securing information regarding the amount

*(More exactly 9.2 bushels).

of difference that should exist between the strains crossed to secure the maximum increase of vigor—self-fertilization of corn inevitably leads to sterility."

Shull has investigated the question of vigor in connection with self-bred strains of corn, originating from the same field mixture, somewhat upon the plan of "Mr. Q. I. Simpson in breeding hogs by the combination of two strains which are only at the highest quality in their first generation, thus making it necessary to go back each year to the original combination, instead of selecting from among the hybrid offspring the stock for continued breeding." Shull's results with hybrids of self-bred strains were similiar to those of Beal, McCluer, and Morrow and Gardner upon hybrids of open pollenated strains, and with which it seems he was not familiar at the time of writing his first two papers on this subject, although in his first paper 72) Shull refers the reader to an article on inbreeding by Shamel in which McCluer's work is mentioned and Morrow and Gardner's experiments are discussed at some length.

Discussing the cause of increased vigor in hybrids, Shull 75) suggests in a recent paper; "the degree of vigor is correlated with the number of characters in respect to which the hybrids are heterozygous—heterozygosis in some elements may be without effect upon vigor, or even depressing. The presence of unpaired genes or the presence of unlike or unequal paired genes, was assumed [A. B. A. 1908] to produce the greater functional activity upon which larger size and greater efficiency depend—East suggests that this stimulation due to hybridity may be analogous to that of ionization—A. B. Bruce proposed that the degree of vigor depends upon the number of dominant elements present rather than upon the number of heterozygous elements."

Since the above propositions are nothing more than theories as yet, other explanations might be considered. Thus, vigor (increased or decreased) might be due to:

(a)—New size-producing factors introduced by hybridazation.

(b)—A new combination of latent size-controlling factors.

(c)—The readjustment necessary in changing from a more or less pure to a complex heterozygous condition which expands or contracts size-producing parts, being therefore a purely mechanical phenomenon similar to the change in form and bulk in many chemical reactions.

In any of these explanations, segregation would have the usual scattering effect upon size in the second hybrid generation.

Again, the theories as held at present in regard to increased vigor may be the reverse of the real truth, and instead of a plant developing above the normal, it may be that by means of favorable combinations the plant is only enabled to develop more or less to its full capacity. A special stimulus may be required to bring out what is perhaps only a small part of the possibilities within its makeup.

INBREEDING.

There seems to be a question lingering in the minds of many as to whether very much self-pollenization takes place in corn. As evidence upon this point, the following observation may be mentioned: An ear having a large percent of sweet (wrinkled) kernels was found growing in a field of dent corn. The seed planted was purchased for pure Reid's Yellow Dent seed. The most probable explanation is: that a grain of pollen from a white sweet corn was blown or carried to the parent "Reid" ear, fertilizing one of its ovules, and because of the two recessive characters—white and wrinkled—possessed by the pollen, the stray kernel was not noticed in the seed since its external appearance was probably much the same as that of the other kernels planted.

It is evident that the ear developing on this hybrid plant was very largely self-pollenated, since the lower three-fourths of the ear exhibited very fair di-hybrid Mendelian proportions in regard to color and composition of the endosperm. That

there may have been a difference in the blooming period of this plant and that of the others surrounding it is recognized, but the upper part of the ear had nearly all smooth kernels due to the effect of dent pollen only, which very probably had come from the surrounding plants after its own tassel no longer furnished pollen.

Ears borne on isolated corn plants are generally reported to have very few kernels 71). In the season of 1910 three isolated corn plants were found growing far apart in a cemetery and each more or less surrounded by trees which served as a wind-break. These plants probably grew from scattered grains in the manure applied to the flower beds. A goodly number of kernels developed on each of these ears, many more than had been expected from earlier observation on isolated plants growing in gardens.

Although these plants were sheltered somewhat, the same conditions frequently exist in an ordinary field of corn, and on a day when there is not much wind a very large amount of self-fertilization must take place. We have frequently obtained perfectly filled, selfed ears by one application of pollen in hand-pollenating work. Such observations prove conclusively the desirability of detasseling corn plants from which seed is to be obtained for general field planting.

Collins 17) has suggested that—"The production of more than one ear on each stalk—would to some extent, correct the tendency to self-pollination, for in practically all cases, the second ear must be cross-pollinated. In regions where high winds prevail at the time of flowering, the percentage of self-fertilized grains would be further reduced." This conclusion was made in connection with a variety in which the anthers made their appearance considerably in advance of the silks. Lazenby 52), however, in what were apparently quite conclusive observations, stated, that "almost without exception the silk appears earlier in comparison with the maturity of the anthers, when there is more than one ear on a stalk."

In our own notes taken daily in 1909, we learned that in some of the varieties producing more than one ear on a plant, the silks on the second and lower shoots appeared very soon after, and in some cases, preceded those on the upper shoot (bagging the upper shoot and leaving the second one exposed frequently favored this apparently abnormal behavior). In general, however, the tendency to mix-pollenate is greatly increased on the lower shoots. This may be the principal reason why seed from nubbins, which often represent ears delayed in development, may produce as good or a better crop the next season than seed produced on large, well developed ears which are more likely to be partially self-pollenated.

In 1905 Shamel 71) reported some observations upon the effect of self-fertilization in corn; "it was found that in four generations of continuous self-fertilization, the vitality had become so weakened that the seed failed to germinate." That Shamel used a strain with an inherent weakness, or that there was some fault in his test, seems to be shown by the results which Shull has been securing on corn selfbred for a number of years. Shull 74) concludes that "the decrease in size and vigor, which accompanies self-fertilization is greatest in the first generation, and becomes less and less in each succeeding generation until a condition is reached in which there is (presumably) no more loss of vigor."

Experiments by East 26) corroborate the conclusions of Shull. East asserts that in a number of families inbred two to four generations; "In all characters of stalks, leaves, roots, male infloresence, and mature seed, the plants were normal. It is merely in the matter of size of plant and ear, and thereby yield, that the plant compares unfavorably with cross-bred plants. Further, there is no continuous decline in yield."

HYBRIDIZATION AND MENDEL'S LAW.

It is essential that the student of heredity have an accurate knowledge of the method of reproduction of the organism in which he is interested. There is no

better way to gain this information than through hybridization, and the final test of a character is to hybridize it. In our study, the work was planned so that certain characters might meet many others in the various hybrid combinations, and that their behavior upon close—and self—breeding might also be determined.

Because of the mass of Mendelian literature, in which the general principles of behavior in combination and segregation have been reviewed again and again, there is no need of their discussion at this place. Since Mendel's Law was rediscovered in connection with a corn hybrid and because of other earlier work upon corn, which has a close relation to this topic, it is worth while to mention some incidents which are of especial significance.

The history of events leading to the rediscovery of Mendel's Law is of absorbing interest and will always stand as a classic example of what patient, thorough search and careful consideration of a vast array of facts and theories accumulated from the work of others may accomplish in throwing light upon a problem in research.

In a bibliography attached to a paper on "Cross-Breeding and Hybridizing" written in 1892, L. H. Bailey included the reference,—(1865 Mendel, G. Versuche uber Pflanzen-Hybriden. Brunn Verhandl iv.-3.47.)
Professor Bailey had taken this reference from Focke's book "Die Pflanzenmischlinge" published in 1881, but had not, himself, seen the paper.

The following is the account in DeVries' own words in a letter to Bailey:— "Many years ago you had the kindness to send me your article on Cross-Breeding and Hybridization of 1892; and I hope it will interest you to know that it was by means of your bibliography therein that I learnt some years afterwards of the existence of Mendel's papers, which now are coming to so high credit. Without your aid, I fear I should not have found them at all."

DeVries had already produced hybrids of sweet and starchy corn in studying the phenomenon of double fertilization in corn. He carried these hybrids through the second generation allowing them to pollenate naturally and reported what we now call "Mendelian segregation" without at first appreciating the significance of it; "Tous ces epis [twenty-five] etaient de nature mixte. Environ un quart des graines etaient sucress, les trois autres quarts etaient amylacess" 81). This was at the time that DeVries was making a thorough search of literature on evolution in preparation for his "Mutations-theorie", a work containing a wealth of references which the author used to such good advantage in establishing this theory. The discovery of the significance of Mendel's paper and its announcement occurred in the year following (1900).

In looking through the available literature upon corn hybridization, other similiar cases are to be found in which Mendelian proportions were approximated, but not being analyzed with due care were consequently disregarded. Ten years previous to DeVries' publication, Kellerman and Swingle 48) noted some results as follows: "The ear consists of about one-fourth sweet corn and the remaining kernels are more or less dented at the summit"—"in the large proportion (probably ¾) of yellow"—"probably seven-eighths of the kernels were flint" and in a later publication 49)—"By actual count, there were 370 kernels on the ear. Of these 206 were blue, 71 pink, 71 orange and yellow, and 22 pure white." Although they did not realize the meaning of these behaviors, they had recorded very fair Mendelian results. It will be noticed that the last quotation contains a very good di-hybrid ratio in which the theoretical expectation would have been approximately 213:71:71:24.

Quoting from McCluer 57); "The self-fertilized ears [of a hybrid] showed the same modification of kernels as those naturally fertilized, proving that each kernel of the crossed corn had in itself the power to produce both sweet and dent corn—the progeny had tended strongly to run back to the parent forms, while at the same time taking on other forms different from either."

In this way the ear of corn had provided most desirable material for the deduction of a general law of inheritance, but was awaiting the insight of a second Gregor Mendel to be made use of. Corn did finally serve for the first corroboration of Mendel's Law in connection with the first announcement of its rediscovery in 1900 by Hugo DeVries.

USEFUL CORRELATIONS.

The Ohio, Nebraska, and Maine Experiment Stations have been making yield tests in selections of certain ear characteristics and have reported but slight differences in results. Davenport, Rietz, and Smith have made use of the statistical method in the study of correlation of characteristics of the ear in a mixed population, and find indications of considerable correlation in some instances. Ewing 31) has recently investigated the correlation of weight of grain with characteristics before or at the beginning of the blooming period, and concluded that aside from the genetic coupling of unit characters, the correlation in the fluctuating variability of two different characteristics is not likely to prove of much assistance to the breeder.

The perfection which Nilsson and his co-workers in Sweden have attained in utilizing character of plant detail in agricultural species has proven highly profitable for economic purposes and has also served as a fruitful source of knowledge in the theory of heredity. Aside from the general use of certain features, such as wrinkled endosperm for table use, large size of plant with relative large amount of ear corn for ensilage purposes, and other similar cases, not a great many distinguishing characters have been made use of in connection with selection for desirable features in corn. The mechanical method used by Hopkins and others in selecting for differences in protein and oil content in the corn kernel is an example of this kind.

It would be desirable to know in a similiar way the possible relations between certain characters which we are beginning to recognize in corn and to have a rather comprehensive list of such characters or genetic units with complete information upon the behavior of each, in order that we may realize more fully the possibilities in the most important American crop. It was with no small degree of satisfaction that this study of the corn plant was undertaken with the knowledge that much that might be learned would be of immediate economic value.

MAIZE GROUPS.

We will perhaps never have positive evidence as to the exact origin of the six generally accepted groups of corn, five of which are distinguished by their endosperm characters. We know that the Indians were cultivating all of them when America was discovered and we can only speculate as to their source. Quoting from Sturtevant 80) ; "It seems almost certain that in the order of evolution (excluding from consideration the puzzling sweet-corn group) progress has been from the pops, through the flints and the dents to the softs." East 25) has suggested that sweet corn "may have come about through mutation in each of these groups [dent and flint], but from what we know of the early sweet corns, it is more likely that the change took place among the flint types and was extended by hybridization."

It seems, however, that there is a much more probable source of sweet corn than the one suggested by East. It is well known that there is perhaps no variety of sweet corn grown that is entirely free from soft starch, aside from the very considerable amount of corneous starch which is always found in all mature sweet corn kernels. There are also varieties of sweet corn which have a semi-starchy endosperm, and Halsted 37) has found that the proportion of starchy endosperm

may be increased by selection in hybrid sweet corn where one of the parents possessed a semi-starchy endosperm. Sturtevant classified samples of such semi-starchy corn received from the Zuni Indians under the name of "amyleasaccharata". As East has also mentioned; many of our varieties of sweet corn have been produced by the selection of segregates from hybrids of sweet with flint, dent, and popcorn and this has resulted in wide differences in kernel shapes, ear and stalk characters.

East's conclusions were based largely on results secured in sweet corn hybrids with flint and dent corns, the new combinations suggesting flint or dent origin, depending on the variety of sweet corn used in the hybrid. In our own observations in 1910, we find that it is possible to get results similiar to those secured by East when we use soft corns to hybridize with the various sweet varieties. Soft corns are quite sweet at the roasting ear stage, and were used by the early settlers for eating from the cob and are still so used to a large extent. The first sweet corn varieties secured from the Indians bore short, eight to twelve rowed ears with broad shallow kernels; these are common characters in soft or "flour" corns, to which considerable evidence points as the source of our sweet or "sugar" corn.

TECHNIC.

In this study, the arrangement and groups recognized by Sturtevant in his bulletin on "Varieties of Corn" 80) were taken arbitrarily for the purpose of classifying and numbering the varieties used.

RECORDING.

A method of numbering somewhat on the plan of the Dewey library system was employed. The six groups were given numbers 100 to 600 and varieties within the groups designated by units. We illustrate the system as follows:—White Pearl Pop was the tenth variety in the list of pop corns (200) and it was given the number "210". It happened that this variety was planted on row 13 in 1909, so in that season the stake and labels on this row bore the field number 210.13. A plant in this row was pollenated by a dent variety grown on row 33, the name and number of which was "Fairview Speckled Dent-404". The hybrid note would then read (210.13-2×404.33-14) and it would also include a description of the work done. The figures following the dash (—2 and —14) indicate the particular plants used on the two rows in making this hybrid.

When the above hybrid was planted in 1910, all of the figures except those indicating the groups 200 and 400 were dropped and as this particular hybrid was planted in row No. 162 in 1910, its field label for that season bore the number 24.162. This was as simple for daily use as the index of the first season and gave all the information necessary for field work. Its previous history could readily be found in the record book of the year before. A reciprocal (404.33-14×210.39-20) of this hybrid was grown on row No. 238 in 1910, consequently its label bore the number 42.238, indicating dent×pop and grown on row 238.

In 1909 the blooming notes were taken daily and for each individual plant, but in 1910 these notes and also those pertaining to the husks were taken every four days, and only for the row as a whole. The observations on size characters and number of parts on the plant were made a short while before maturity, and the observations on the ears were all taken in the field at harvesting time, the study of kernel characters being left for the laboratory. In general, such characters were chosen which could be recorded readily. Many interesting and desirable features were neglected entirely for lack of time.

POLLINATING.

Some methods of technic were developed during the experience of the two seasons, a knowledge of which would have been of much value in the beginning.

As some of these may be of use to others contemplating similiar work, brief mention will be made of a few of them.

The record books should always provide room for special or general notes upon an individual or row in addition to the regular scheme. The labels used for marking plants should be such as will not be destroyed by wind and rain. Cloth, wood, or metal labels with a wire tie are indispensable.

In a locality where storms are apt to occur when the corn is in bloom, tough parchment paper bags are necessary to protect the shoots, but ordinary manila bags will serve to collect pollen. Parchment paper is desirable because of its semi-transparency, which allows observations on the color and especially on the development of the silk without removing the bag. This is very convenient at pollenating time. The most satisfactory and expeditious method of bagging shoots was that of bending down or preferably breaking off the leaf blade in the sheath of which the shoot to be pollenated is developing. The inverted bag with one side between the shoot and the culm is then pulled down over the shoot with a sawing motion till there is room to fasten the bag to the leaf sheath, or to the shoot about which it is folded, with an ordinary brass pin. A flexible wire may be used to split the leaf sheath in case the bag is not strong enough to accomplish this with ease. The bagging of shoots must be done, of course, before there is any indication of a silk and the bag should be left on ten to fifteen days after the silk has been pollenated. In a moist climate these shoot bags should be removed when all danger of contamination is past, since the developing ears tend to become moulded when the bags are left on.

The bags for collecting pollen were put on early in the morning of the day in which the pollen was to be used, preferably before the pollen begins to fall, because there is here a possibility of collecting stray pollen grains which have lodged on the tassel from surrounding plants. In a dry period, this may be quite effectively guarded against by bagging the tassel on the day preceding, as, in the majority of cases, corn pollen is no longer viable in from 24 to 36 hours after it has been shed. For this reason best results are obtained in pollenating work when pollen is used within a few hours or during the same day on which it has been gathered.

The inverted pollen bag is readily fastened about the base of the tassel by means of a spring clothes-pin, which is a very handy article in general plant-breeding work. The bag is fastened in such a manner that one side is lower than the opening, thus providing a pocket in which the pollen may lodge instead of sifting out through the crevices at the mouth of the bag. In this way sufficient pollen may be secured at one time from one tassel to pollenate a number of shoots. The pollen may be used at any time of the day and in all kinds of weather, so long as the pollen and silks are kept reasonably dry. Studies made on the behavior of pollen and silks will be discussed in connection with the inflorescence.

In case the silk came in contact with the hands or apparatus in the process of pollenating it was carefully clipped with scissors. In general and except for special study, all the silks were clipped at a short distance above the shoot as the bag was being removed from it. When a shoot is young it may be clipped below the tip and opened, thus exposing a larger number of silks. Clipping of silks was done not only for ease in operation, but also to insure thorough application of the pollen; clipping also prevents heating of the mass after the pollen has been applied. When long and tangled silks are pollenated barren patches on the cob are frequent because of the pollen failing to reach the silks on the inner or lower side and sometimes due to the heating mentioned. The pollen is poured directly from the bag and thus the silk and the pollen are never touched by the hands, except by accident. There is therefore no need of washing the hands in alcohol after each

pollenation, as some workers recommend. The scissors used in clipping, and the hands of the operator as well, may be cleaned with the silks which are cut away.

Some workers expose the shoots while pollenating them; others use an umbrella with or without a side curtain for protection from falling pollen, the umbrella having an extra covering to make it pollen proof; for extensive work, this requires an extra man to hold the apparatus and is, at best, not very satisfactory. During the first season, a pollenating apparatus was used which was cylindrical in shape, mounted on a pedestal, covered with oilcloth, and large enough to admit the operator. A slit was made in the curtain to admit the lower part of the plant including the bagged shoot. On warm days, continuous work in this cloth cage was very trying and a new apparatus was constructed for use in the second season.

The new apparatus consisted of an inverted box of very light wood, which had been carefully seasoned to prevent checking, all the joins being sealed with glue. A short curtain was attached about the base to exclude falling pollen. The box was large enough to provide room for the manipulation of the pollen and silk, all but the arms of the operator being on the outside. The side of the curtain, inserted between the shoot and the culm, was provided with a metal shield having a narrow "A" shaped opening and sewed into the heavy duck curtain. In the box and just above this opening was inserted a pane of glass to provide light. Glass panes were also placed in the side opposite and in the top of the box. In this way the operator is enabled to view his work from a number of directions, according to the height of the shoot. The box was readily adjustable to any height on an upright rod mounted on a "T" base with recurved sharp points to anchor it in the soil and to allow it to be readily removed. These points were long enough to permit straddling the ridge usually thrown up along the corn row in cultivation.

In order to secure pollen from an early blooming variety to use on a late blooming variety, it was necessary to make several plantings. It was found, however, that the late plantings matured much more quickly, relatively, than the earlier planted rows. It was frequently necessary to use the last tassels to mature on the early varieties and these were found on poorly developed plants or on suckers. This practice introduces difficulties in the interpretation of the results. We may have thus selected genetic differences in sucker devlopment, but otherwise the use of pollen from suckers would not be expected (of itself) to seriously affect results. Hartley 41) states that progeny from ears fertilized with pollen from suckers were as productive as plants from ears fertilized with pollen from the main culm. In general, only one application of pollen to each shoot was made. The practice of pollenating the same shoot several times is not only time consuming, but also allows more opportunities for mixture by stray pollen grains.

East 27) has experienced difficulty in getting certain varieties to hybridize and has concluded that there are some varieties which will not combine with others. Similar experiences have been reported by early investigators. Collins 18) and Emmerson 29) have later secured successful hybrids with strains similar to those used by East. In my own work, wherever I was sure of the viability of both pollen and silk, I have found no difficulty in securing hybrids between varieties differing widely in regard to size, period of growth, and many other characteristics.

TERMINOLOGY.

Confusion exists in literature regarding the meaning of the words "hybrid", "cross", and "inbred". At present the terms "hybrid" and "cross" are used interchangeably, some writers using both words in the same sentence in referring to the same individuals. While these superfluities of the language are permitted; they are confusing, especially to the uninitiated. In this work some distinction was necessary and the terms will be used throughout the report as defined below:

Substantive.	*Infinitive.*	*Definition.*
a hybrid	to hybrid	to interpollenate individuals of distinct varieties or species (so called).
a cross	to cross	to interpollenate individuals of strains or "lines" of the same variety.
a close	to close	to interpollenate individuals springing from the same flower or mother plant.
a self	to self	to pollenate with pollen from the same flower—or other flower—on the same plant.
a mix	to mix	to pollenate with pollen from either an unknown or hetrogenous source (this applies to individuals pollenated naturally in mixed populations).

The above terms are in common use and the distinction here made is no radical departure. Although the ardent supporters of the "genotype" ideals might maintain that there is no difference between hybrids and crosses, some distinction should be made between a sweet corn$\times$rice pop hybrid, as an instance, and a cross between strains of slight differentiation coming from a well established variety like Reid's Yellow Dent or Boon County White corn. The general term "wide bred" will be applied to hybrids and crosses; the general term "inbred", which has been confused in a number of papers with "selfbred", will be applied to closes and selfs.

The sign "$\times$" is to be interpreted as it is commonly used; meaning, "pollenated with", when inserted between two variety names or numbers. The sign "$\bar{\times}$" will be used in the tables to indicate hybrids which have reciprocals. The expressions F (or F_0), F_1, F_2, F_3, etc., are being used in papers dealing with Mendelian segregation, the letter "F" being an abbreviation of the word "filial". In discussions concerning the progeny, the words "hybrid generation" are used and not "filial generation". In reports on segregation, it is not unusual to find the expletives "F_1 hybrid generation", "F_1 generation of the cross", etc., in dealing with hybrids only.

By those who begin the use of the "F" expression and by those who are at present employing it, a new term may not be desired, and at this late date a change may be somewhat confusing; but in themselves the expressions $\times$, $\times_1$, $\times_2$ $\times_3$, etc., would be intelligible almost without explanation, since the sign "$\times$" is in common use in discussions concerning reproduction. Because we have need of the letter "F" in a number of cases to designate characters in discussing segreates and parents in corn, the above suggested expressions will be used in this report. The term "$\times$generation" will always be used in referring to the seed produced by the parent plant. When that seed has germinated, the plant developing from it will be designated "$\times_1$ generation", its seed and the plants resulting therefrom as "$\times_2$ generation", the succeeding generations as "$\times_3$", etc. By the word "seed", in this instance, we refer to the germ and endosperm only and not to the seed coat which is tissue identical with that of the generation preceding the new seed We will apply the expression "$\times$", etc.* to the progeny of hybrids, crosses, closes, and selfs; and whenever it becomes necessary to discuss two or more of these classes of reproduction simultaneously or in review, it will also be necessary to include the name of the class to which reference is being made.

*Since this paper was submitted for publication the writer has learned that Lotsy (Biol. Centralblatt 25:97-117) has employed the expressions "x-generation" and "2x-generation" as substitutes for "F_1" and "F_2". It seems, however, that the expressions "x", "x_1", "x_2" are more appropriate since they suggest only relative or subsequent generations rather than giving the idea of increasing complexity or hybridization only, as Lotsy's "2x—" and "3x—" terms would imply.

Those who are familiar with variation in corn will appreciate the handicap under which this work was started, with no inbred strains, and many of the varieties imported. These difficulties are especially perplexing in the plant characters to which very little attention has been paid in the developing of new varieties and strains. From an economic standpoint, the significance of *plant* or "stalk" characters was not recognized until quite recently. This fact accounts to a large extent, for the individual variation in *plant* characters. Differences are often as great within a variety as between distinct varieties whose classification is based largely upon *kernel* and *ear* characters.

GERMINATION

A number of influences within the corn kernel affect germination and the early growth of the seedling. Some individual ears and also varieties exhibit a much more vigorous germination than others. It has been observed that some of the high yielding varieties frequently germinate poorly and this has been associated with the old mistaken idea, prevalent among animal breeders at one time, that improved strains showed the often observed loss of "vitality" as a direct consequence of the "improvement". We know now, that vitality was lost in some of these cases by selecting the wrong segregates. It is also evident that many economically desirable characteristics in plants and animals are in a sense degeneration, in that they are not favorable to the perpetuation of the species except by the intervention of man. It is well known that single-eared and high-yielding varieties tend to have deep, closely packed kernels and mature late. Such ears do not dry out well, are apt to ferment and mould, and therefore germinate poorly or not at all.

It has been noticed that starchy kernels are apt to germinate more quickly than hard, flinty kernels of the same variety. In germination, the scutellum or cotyledon (the organ in which enzyme secretion takes place) uses the soft-starch portion of the endosperm first and the horny portions, if there are any, are used more slowly. A soft-starchy endosperm thus furnishes the more available food and should favor a more rapid development of the germ. In order to test this theory a number of $\times_2$ kernels from hybrids of flint, soft, and sweet corn were germinated in flats of soil in the laboratory. In this way two and, in some cases, three of the above types of kernels could be obtained from the same hybrid ear. All the kernels were planted at exactly the same depth by means of a wood pin having a collar to permit uniform planting through a heavy wire screen placed on the surface of the soil. This method insured accuracy in spacing as well as in depth of planting.

In the majority of cases, grown in the laboratory, the starchy kernels slightly preceded the flinty kernels in germination, but the difference was not especially noticeable and the resulting seedlings were quite similar in height and vigor. The most noticeable difference was between either starchy or flint as compared to sweet kernels which contain very little soft starch. Plumules from the wrinkled kernels first appeared above the soil at from 10 to 24 hours later than those from either the starchy or the flint kernels, and the germination of the entire lot of sweet kernels was extended over a much longer period of time.

The delayed and often lower percentage of germination of the wrinkled kernels may be associated with the fact that wrinkled kernels mature later than starchy and flinty kernels on the same heterozygate ear. This is very noticeable in the field just before the corn ripens; at this time the kernels which become wrinkled later are larger and much softer than the others on the same ear. This has been noticed also by Halsted of the New Jersey Experiment Station 37). Still another explanation must be considered. Segregation in rapidity of growth factors may

have taken place in these $\times_2$ kernels borne on $\times_1$ cobs and there may or may not be an association of this behavior with a character in the endosperm.

Walls 84) selected kernels with large and small germs, finding that "the heaviest grains do not necessarily have the best germinating qualities—The germinating properties of the kernels containing different sizes of germs may be equal."

Correns 19) stated that he observed no change in rapidity of germination of the $\times$ hybrid seeds. In our own work, however, we noticed that in general, the $\times$ hybrid seeds gave a more rapid germination than the parents. In a number of cases, these hybrid plantlets were more vigorous and maintained a larger size throughout the season. For lack of time we were unable to get exact field data on germination in 1910, but during the last winter several sets of observations were made in the laboratory in connection with other tests on the influence of the endosperm on early growth and on which the above conclusions were based.

Indications were found that popcorn pollenated with other groups germinated better than other groups pollenated with popcorn, while popcorn alone gave in some cases a better germination than the other groups. In corroboration we may cite Sturtevant and others who have reported that popcorn has a better viability than the other groups. This may be due largely to the adaptation in kernel shape, composition of seed coat and endosperm of the pop group.

The specific density is not always a safe guide to the viability of a corn kernel, as was shown in a case of a partially constricted ear.

Less than a fifth of this ear was normally developed at its base, the remainder being abruptly smaller as if the whole ear had been developed and pollenated normally and then the nourishment cut off very suddenly from the upper four-fifths. It was at first thought useless to plant any of the small shrunken kernels in the field, but it was decided to give them a trial. Thirty hills were planted with the large kernels and twenty hills with the small shrunken kernels. To our surprise, every kernel grew and the viability of other kernels from the same ear remained nearly as good a year later as shown by a germination test. The small kernels germinated more slowly and there was a marked difference in the size of the young plants, this difference diminishing somewhat as the plants grew older. The average comparative sizes of 100 kernels from each of the two parts of the ear near the division line were:

	Av. Wt. of 1 kernel (gms.).	Av. Vol. of 1 kernel (cc.).	Av. specific density of 1 kernel.
Large Kernels	0.321	0.256	1.25
Small Kernels	0.112	0.101	1.11

The following data represents the empirical modes of 29 plants grown from the large kernels and 19 plants grown from the small kernels:

	Height of plant (in.)	No. of apparent internodes	No. internodes below the ear	No. of shoots	No. of ears	Length of ears (in.).	Cir. of ears (in.).	No. of kernel rows	Growing period (days).
Large Kernels.......	110	16	9	2—	1	8.—	6.5	20	123
Small Kernels.......	100	15	9—	1	1	8.—	6.0—	20	127

The data just given will serve two purposes:—To illustrate that the hereditary make-up of the small kernels, which was probably the same as that of the larger ones, enabled the plants by the end of the season to catch up with the plants from the large kernels in three out of nine more or less fluctuating characters. On the other hand the data serve to point out the effect of what are perhaps only

physiological or somatic difference in the kernels. These differences apparent in the kernel and in the plantlet stage are not entirely overcome but have their effect throughout the life history of the plants in which the genetic make-up was probably identical.

The permanent root systems of Gemineae develop from the stem and at or near the surface of the soil. Thus, no matter at what depth a kernel of corn is planted—if the depth is not excessive—the epicotyl lengthens until the node at the base of the coleoptile is near the surface in dry soil, or at the surface in wet soil, before the secondary roots develop. The kernel itself remains hypogeal. After these secondary roots have become established, the primary root is of little or no value to the plant.

In germination, other temporary roots develop from the placenta of the germ. In our observations, we have found these to vary from 0 to 8 in number, some of them arising from between the epicotyl and scutellum, the remainder from the outside. In tests with from 20 to 30 seedlings, from each of 67 individual hand-pollenated ears in various varieties, we found differences in modal numbers of from 0 to 4 of these rootlets. The counts were made on young plantlets from seeds which had been in soil two weeks.

That these roots play a vital part in the young plantlet stage cannot be questioned, as they often take the place of the primary root which may become diseased, cut off by insects, or fail to develop. What relation they bear, if any, to the mature plants or how they behave on hybridization has not been determined. Numerous, small, temporary roots may also develop on the epicotyl (below the first node.)

PLANTLETS.

It is always of great practical importance in plant breeding to be able to recognize in the seedling stage of a plant what its adult characteristics will be DeVries 82, 83) has made much of this point and cites a large number of instances in which characters in the seedling are correlated with characters which become apparent later in the mature plant. The extended use which Luther Burbank and other plant breeders have made of seedling characters in eliminating undesirables is well known.

It was hoped that a number of distinct characters might be found in seedling corn plants and from the limited studies made it is apparent that quite a large list of such characters exists. Among the varieties red tinge stems develop soon after germination. This character is correlated with red tinge on the mature plant in some varieties. These are constant when homozygous, and dominant to pure green stems.*

Dark green leaves are distinct from light green leaves and the X_1 hybrid plantlets show dark green. Very narrow and very broad leafed seedlings are constant when homozygous. Certain dents and flints show very broad, blunt seedling leaves, while rice pops illustrate best the narrow pointed grass-like form. Broad leaves appeared in the X_1 hybrid seedlings between the types. Plantlets from closed and selfed ears in one strain showed marked differences in leaf-shape.

Large size of parts is dominant to small size in X_1 plantlets as well as being an indication of increased vigor. A number of plantlet abnormalities were found but their genetic relation has not been learned.

ALBINISM.

Albinism, partial or complete, occurs in many species of plants and animals and, although its cause has not been determined, its behavior has been quite well

*We will designate characters as dominant when they are epistatic to another in the x_1 generation. The ratio or "type" of segregation for the "*plant*" characters is, of course, not determined at the time at which this paper is written.

studied in a number of cases. Miss Newbegin 64) found a diminished capacity for assimilation in plant albinos and thus the phenomenon might be explained as a degeneration. That it is not a consequence of the artificial conditions of cultivation is shown by the fact that many cases have been observed in nature. DeVries 83) recites a number of examples arising as seedlings and bud variations from green or colored ancestors to which they are more or less recessive, and generally inconstant in themselves.

Cuenot 21) found albinism to be a recessive character in mice. Farabee 32) gave an account of negro albinism which indicates this character being recessive in man. Castle and Allen 13) report a similiar behavior in rabbits and guinea pigs and state that "complete albinism, without a recorded exception, behaves as a recessive character in heredity." Others have investigated various degrees of albinism and so far as known, with one possible exception in axolotl, reported by Haecker, the statement by Castle is true of albinism in its pure state. The behavior of white pigment, which seems to be complicated, is not to be regarded as albinism.

Bateson 3) describes results of his own and other investigators in which the hybrids from two sweet pea parents with white flowers have all been colored in the $\times_1$ generation, the $\times_2$ splitting into the dihybrid (9:7) ratio. This behavior is explained as due to the meeting of a complementary character from each parent, producing no color when separated.

Corn in which albinism exists in the pure state cannot live beyond the plantlet stage (3 to 4 leaves) since the young plants cannot elaborate plant food because of the absence of chlorophyll. Bauer 5) reports a similiar behavior in pure albino seedlings arising from white margined and partial albinos in geranium.

Albinos are not uncommon in corn, but so far as known there are only three published reports of actual counts in which close-bred or hand-pollenated seed was used. The first case was that found by Hastead 35) in the $\times_2$ generation of Black Mexican and Egyptian sweet corn parents. No white plantlets were found in the germination tests of the parents. By various treatments he found that the proportion of albinos could not be affected. It was also found that both ears from the same stalk, with one exception, produced albinos, and that the character was therefore "within the plant".

The important test made by Halsted was that in which "inbred" (probably selfbred) and "wide bred" (probably hybrid) seed was used from the strain in which the number of albinos was pronounced. His counts were as follows (ratios computed from Halsted's data):

Selfed (?) corn.	Albinos.	Green.	Ratio.	Per cent. albinos.
Ear No. 1	13	47	1:3.6	21.7
Ear No. 2	15	38	1:2.5	28.3
Ear No. 3	7	48	1:7.0	14.6
Hybrid (?) corn.	**Albinos.**	**Green.**	**Ratio.**	**Per cent. albinos.**
Ear No. 1	0	60	...	..
Ear No. 2	0	65	..	.
Ear No. 3	0	65	...	..

This was soon after the rediscovery of Mendel's Law and Dr. Halsted was probably not studying his hybrids in sweet corn with regard to Mendelian segregation at that time. Although he has been making use of this all important law in his hybridizing work since, we have not found that he has corrected his conclusions upon this phenomenon, namely,—that close fertilization was probably the cause of albinism.

It is plainly evident that he secured on the first two ears, with only 60 and 53 kernels germinated, very nearly the simple Mendelian ratio with the percent of albinos 21.7 and 28.3, rspectively, and an average for the two of 24.8 per cent. The distribution of albinos on the third "inbred" ear must have been very uneven from the charatcer of the results obtained and should be discarded. When it is included, we yet have the very satisfactory average of 26.3 per cent. albinos in 133 kernels from three ears. On the opposite page in Dr. Halsted's report may be found an interesting photograph of these three lots of plantlets by the side of the three lots of "widebred" (hybrid?) green plantlets. This photograph not only shows the dominance of green to albino but also, shows very strikingly, the increase in vigor in the hybrids, a phenomenon which has since become so important in the development of the theory of corn breeding.

Blaringhem 9) noted an instance of five albinos in 37 plantlets from a mutilated parent of flint corn which was probably close pollenated. He also reported finding the albinos from year to year in his various cultures. Collins 18) found nine albinos in 48 plantlets of a hand-pollenated ear (close-bred) of dent corn, while the hybrid of this with another variety produced green plantlets only. Evidently neither of these cases were studied with any thought of Mendelian segregation, and the counts reported are very limited but all point to the conclusion that they were dealing with a simple Mendelian ratio.

Dr. Smith has observed during the last few seasons an increasing proportion of albino plantlets in the "low ear strain" of yellow dent corn grown at the Illinois Experiment Station and in the season of 1910, two ears were secured from this strain for use in this experiment upon inheritance. The two ears came from parents which showed a large per cent. of albinos in 1909. A number of plants grown from these ears were selfbred and closebred as well as hybridized with other varieties including some with variegated or striped foliage.

As a preliminary test, 100 or more kernels from ears obtained in 1910 were planted in flats of soil in the laboratory, 10 selfed, four closed, and six hybrid ears were used. Only green plantlets were produced from four of the selfs, three of the closes, and six, or all of the hybrids. From the remaining six selfs and one close, the following proportions of green and albino plantlets were obtained:

Fig. 1.—Albinism in young corn plantlets. One of the rows in the germinating box which gave exact 3:1 ratios of greens and albinos.

SEGREGATION OF GREEN AND ALBINO PLANTLETS.

	Greens.	Albinos.	Ratio	Per cent. of albinos	Number of plantlets.
424.60×S	104	27	3.9:1	21	131
424.59×S	76	29	2.6:1	28	105
424.59×S	82	20	4.1:1	20	102
424.59×S	72	16	4.5:1	18	88
424.59×S	61	15	4.1:1	20	76
424.59×S	76	23	3.3:1	23	99
424.60×C	75	29	2.6:1	28	104
Total	546	159	av.=3.4:1	av.=23	705

These cases, averaging 100 kernels from each ear, show conclusively that albinism in corn is a simple Mendelian recessive. The character is especially interesting from the theoretical as well as the economic side. It is brought to view in the homozygous state only, and in this condition is disastrous to its perpetuation; therefore the only way it can be transmitted is in the heterozygote. It is apparently due to the absence of the factor which in the green plants produces the chlorophyl.

What appears to be an intermediate stage of albinism was found on an ear which was selfed and produced 20 yellowish greens and no albinos in 100 plantlets. The first test of this ear with only 64 seedlings gave 16 yellowish greens or 23.9 per cent., which is near the theoretical proportion. The final test of 3 plantlets gave only four yellowish green individuals, and this poor distribution caused the total proportion of 4:1, or 20 per cent. yellowish greens to fall short of the theoretical, although it is evident that "yellowish green" is also a true recessive. These two characters, albinism and the yellowish green, which may be an intermediate form of albinism may be added to our list of those characters appearing in the plantlet stage.

SUCKERS.

The idea prevails generally that the ancestor of corn was a much branched grass. Harshberger 38) suggested that—"the original form in the wild state was propagated probably by lateral offshoots—The habit of suckering, annual in the north, was probably perrenial in a more southern latitude, so that in the semi-tropics the non-sexual development of suckers was the ordinary method of propagation, the vigor of the stock being rejuvinated by an occasional distribution of seed by birds." Under favorable conditions most of the commonly grown varieties produce suckers.

The tendency to sucker or tiller is decreased as a variety characteristic in the corns developing stout stalks, and those varieties growing to extreme height produce few or no suckers under ordinary conditions. There seems also to be a decrease in number of suckers in those varieties which produce very large ears or cobs. This variation in number of suckers is so noticeable that there is apparently a direct correlation with the above mentioned characters but modified by thickness of planting and other environmental influences. Dense planting, unfertile soil, low humidity, and excessive heat, all have a direct limiting effect on the development of suckers, while inbreeding and consequent decrease in vigor also tend to check their development.

Occasionally an individual plant is found, apparently constant otherwise, that stands out from among its fellows in the production of suckers or other vegetative growth and this is frequently attributed to reversion. Collins 15) has published an

account of apogamy in corn in the form of plant like branches developing from pistillate flowers in the tassel and producing short aerial roots while attached to their place or origin. These branches, when removed and placed in soil, produced roots over a foot in length and growth continued in an apparently normal manner for nearly two months.

Suckers may begin to develop on corn when the seedlings are less than a foot in heigth. Later, in certain varieties and especially under adverse conditions, some or all of these young suckers may wither and die. Those suckers that start at or beneath the surface of the soil and live through the season, develop strong, independent root systems and frequently become separated from the main stalk due to the expansion in growth and rupture or death of the connecting strand.

In a test concerning the value of suckers in dent corn, the Nebraska Experiment Station 56) reported an average loss in two consecutive seasons of 17 bushels per acre when the suckers were removed. Similar results were reported later 61) by the same station. They found that "Removing tillers has had a tendency also to increase the number of two-eared stalks and decrease the number of barren plants, although this benefit has not apparently been enough to counteract loss of ears ordinarily produced by tillers." In these results it was evident that the production of suckers was an adjustment on the part of the plant to existing conditions, the suckers' developing when there was room and nutrition, disappearing when there was not. The best yielding rows always had a good percentage of ear-bearing suckers. Card 12), of the Rhode Island station, selected plants with the largest total number of ears in a variety of sweet corn and found that this was associated with the production of a large number of suckers.

It is doubtful whether suckers ever have much value to the main culm since they at first receive nourishment from it and, later, after they have developed their own root system, feed in the same soil mass, thus robbing the main part of the plant continually. Lyon 55) and Hartley 41) report wide variation in the production of suckers in dent corn, also that it is hereditary and can be controlled by proper selection and breeding.*

During the two years in which they were under observation, several of the strains and their hybrids produced no suckers; But, perhaps, every variety known will produce some suckers under certain conditions. All degrees from non-suckering to profuse suckering were found.

In the hybrid ($\times_1$) the minus-fluctuations (diminished sucker production) appeared to be dominant to the plus fluctuations (profuse suckering). An absolutely non-suckering behavior would be expected to be dominant to a suckering behavior. Suckering depends very largely on environment and vigor.

Comparing these $\times_1$ results with published accounts of tillering and branching in other plant hybrids, we find that Keyser 50) reports a wheat hybrid in which the stooling was more abundant than with either parent. Bateson et al 3) states that the much-branched, erect habit of the "Bush" Sweet Pea is evidently recessive to the unbranched form. Shull 73) found a branched sunflower to be dominant

*Ninety-nine varieties and strains, representing the six species-groups, were used in the experimental work in preparation for this thesis. The greater proportion of these strains of corn used were found to be complex mixtures and in the second year many divisions were made of the list as it was used at the beginning of the work.

The arrays of varieties in the parents and their hybrids, as well as the empirical modes and summaries of the arrays, were tabulated in order to gain a definite idea of the constancy of the character in question as well as the nature and limits of fluctuation if any variation was found. Two generations of the parents and only one generation of the hybrids, selfs, and closes ($\times_1$) were grown.

In the tabulation of data no aberrant individuals or populations were discarded at any time for lack of conformity to the bulk of the array or table. Selections were made for a wide range in combinations of characters. The hybrids, selfs, and closes, all came from carefully controlled, hand-pollenated seed produced in 1909.

This tabular matter and discussion of it have been omitted in this paper and will be substituted by brief general statements concerning the results.

to the unbranched. Balls 2) includes "branching base" in his list of dominant characters in the cotton plant. Saunders (cit. Bateson 3) gave the branched form of stocks as dominant to an unbranched type. While Keyser's case in wheat is the only one directly comparable to tillering in corn, there was no total absence of tillers and perhaps no genetic difference in the parents with respect to this character, and the increased stooling in the hybrid may have been due merely to increased vigor. It might also have been due largely to the conditions under which the hybrid was grown.

LEAVES.

During the growing season many noticeable differences in leaf characters are to be found, such as; the arrangement, shape, texture, color, pubescence, vienation, and sheath characters. The misroscope would no doubt aid in identifying many others in addition to those mentioned.

A corn plant may give a general impression of "leafiness" from several causes—alone or combined. A broad or long leaf may give it this characteristic appearance; but it is more often due to a relatively large number of leaf nodes on a short stem, which is equivalent to very short internodes. Suckers would naturally tend to give it the same appearance. Since number of leaves is determined by the number of nodes or internodes, except in rare cases where there are two or more leaves at the same node, its behavior will be identical with "number of internodes", to be discussed later.

LEAF ARRANGEMENT.

Perhaps the most noticeable differences in aspect of the leaves are found soon after blooming time when they are nearly developed, but still fresh and succulent. *Zea mays* exhibits the characteristic alternative, two-ranked leaf arrangement of the Gramineae. Twisting occurs in the upper and more slender parts of the stem, so that frequently the leaves above the ear are not in line with the lower ones nor exactly on opposite sides of the stem near the tassel. In a number of cases the leaves near the tassel are all warped to one side of the stem.

It is not uncommon to find plants having two or more leaves at the first and second nodes below the tassel. These abnormal leaves are narrow and diminished in size, giving the appearance of division rather than of addition of parts. Blaringhem 9) has noted a shortening or telescoping of internodes below the tassel on poorly developed adventitious suckers produced by traumatism. Evidently these abnormal growths represented efforts on the part of the mutliated plant to perpetuate the species, which resulted in a contorted stem with a tufted arrangement of leaves.

In the plants observed here in Illinois in the two seasons, only one of the cases of prolification was associated with a deformity of the plant itself and in this instance the two nodes immediately above the soil each bore a pair of leaves. Although this plant had only one less internode than the empirical mode of the row, it attained but little over one-half the modal height. This, and most of the cases of pairing of leaves on the first or second node below the tassel, occurred upon $\times_1$ hybrids. Three cases were observed on corn that had been selfbred for a number of generations, one of these plants producing three leaves at the first node below the tassel. The plants observed were generally of average height and number of internodes, more frequently above than below the average. These cases, therefore, cannot be explained as being due to telescoping nor to fusion of two nodes, but are simple cases of prolification or merism, the cause of which is unknown.

During the season of 1910, a plant of rice popcorn was found having several suckers, all normal but one which had paired opposite leaves at every node; thirteen

pairs in all. There was a shoot in each of the axils of these paired leaves at the eighth, ninth, tenth, and eleventh internodes above the soil. It is not expected that such abnormalities are inherited.

Stray individuals having very erect leaves occur in a number of varieties. The erect leaf accompanied by a one-sided arrangement about the tassel is noticeable in corn which fails to develop fully. The one-sided position of leaves near the tassel is frequently associated with very short internodes in that region. During the season of 1910, a one-sided arrangement of husks was found to be frequent on mature corn in general field culture and it is possible that such cases of orientation of leaves are due to warping.

Collins 18) in a paper concerning hybrids between a "Chinese corn" and other varieties, reports that the erect monosticious blades seemed dominant in the $\times_1$ generation hybrids at first, but later in the season the character was not so marked. Second year plants from the original seed did not have this character so strongly developed.

Mr. Collins kindly furnished some of the original seed for a test here at the Illinois Station, where it was grown in 1910, and a large number of the plants behaved as described in Mr. Collins' original paper. It was noticed that the leaves on the plants grown here in Illinois were inclined to be thick and rigid. It is possible that after it has become acclimated, this variety will still retain an erect position of leaves somewhat above the average, as other varieties possessing rigid leaves with heavy mid ribs tend to do. Blaringhem 9) in his paper on traumatism, figures the tassel and upper leaves of what he considered to be the normal type of a yellow flint variety, which exhibited this erect position of upper leaves at blooming time.

A violent storm on August 23rd, 1910, ruined the entire field for observations on leaf arrangement. On many of the plants, which had not been broken off, only the midribs of the leaves remained. The difference in position of these midribs when stripped of the leaf blades was very noticeable. In general, $\times_1$ hybrids have larger, broader leaves, consequently a heavier leaf load than the smaller of the parents; but the rigid thickened blade and midrib is also, apparently, a dominant character and tends to give the leaves an erect appearance.

Some varieties have very much smaller leaf blades near the tassel than those lower on the stem, thus giving an open, sparse effect; other varieties have relatively large and broad leaves near the tassel frequently accompanied by shortened internodes. This latter condition gives a dense, crowded effect and although long internodes are apparently dominant, large leaves are also dominant and various $\times_1$ hybrids exhibit this leafy appearance about the tassel.

LEAF SHAPE.

Perhaps no two leaves on a single plant of any species are alike in outline. Usually on the corn plant there is a gradual increase in length and leaf area till the upper ear-bearing node is reached, and then a rapid decrease in leaf dimension occurs until the upper leaf at the tassel-bearing node is reached. In some varieties the upper leaf is often but a mere bract, while in others this leaf is quite broad, but much shortened in comparison to the leaves at the middle of the stem.

Very long leaves and very broad leaves are prominent characters of some varieties and strains. Hartley 39) found a broad leafed plant of dent corn in 1900 which he selfed, and in 1901 the progeny was very noticeable because of their broad leaves, many being six inches in width. Seed from this row planted in 1902 produced plants which exhibited the same character. Collins 18) reports a hybrid in which the leaf blades were slightly shorter but much broader than those of either parent.

General notes only were taken in leaf shape in this study. Varieties with characteristics of different dimension in length and width were found. Several hybrid rows, the product of parents one of which had long leaves, were noted as having very long leaves. A number of hybrids with a broad leafed dent variety also bore broad leaves. Largeness, including both dimensions, is dominant to the mediocre or small leaf. Leaf blades with a broad base are apparently dominant to those with a narrow base.

Abnormal leaf shapes were frequently found. Many of the hybrids as well as the parents produced cleft and distorted blades. Cleft leaves were found more often on suckers than on the main clum. Blaringhem reported tubular and cleft leaves developing on mutilated plants, and stated that the tubular development was reproduced to a considerable extent from year to year on these weakened strains. DeVries 83) has pointed out associations of cleft leaves with other monstrosities, such as fasciations and twisted stems in various species.

LEAF TEXTURE.

Certain external differences in leaf structure occur which serve to distinguish varieties as well as individuals. Among these differences which are apparent without miscrscopic study, are rough and smooth leaves—without reference to pubescence; thick, rigid blades in contrast to others which are thin and wavy, sometimes crinkled. In a number of X_1 hybrids the rough and the rigid types were dominant to their opposites.

During the season of 1910 a small variety of white rice pop produced crumpled leaves throughout. The leaf sheaths and bases of the blades, especially, gave the appearance of having been crushed or jammed in the process of development. No hybrids involving this character have yet been grown. Collins 18) noted a hybrid between Tom Thumb pop and a tall Guatemala variety, all the plants of which had crumpled and distorted leaves.

DISEASE RESISTANCE.

Disease resistance in plants is of great economic importance and remarkable cases are on record of the finding of single plants which withstood attacks of fungi when all their neighbors have been destroyed by the disease. Such cases have been taken advantage of in a number of species 65). The production of antitoxin in these disease resistant plants has been suggested as an explanation of the behavior.

Rust resistance was found to be a recessive character in wheat by Biffen 8), but so far as known no other cases have been reported in which this character has been studied with regard to segregation in the hybrids, although a number of cases have been reported of selection of disease resistant plants after hybridization.

66). This last mentioned fact seems to indicate that disease resistance is generally a recessive character. Shull 72) reported increased susceptibility to smut on self bred corn plants.

In 1910 we noticed a number of plants which were seriously infested with rust while others were practically immune. Very little rust was noticed in the previous season which was a very dry year. A hybrid row in 1910 showed advanced stages of rust (probably *Puccinia sorghi*) on every plant. Another X_1 hybrid row containing only sixteen plants produced six normal green individuals which bore small ears, while the leaf tissue of the remaining ten plants was thickly studded with large pale yellow spots turning later to a darker yellow. These diseased plants were smaller and more slender than the green plants and none produced ears. The nature of the disease has not been determined.

It may be that disease susceptible combinations were unwittingly made in these two hybrid cases and that in the latter case we secured what appears to be segrega-

tion. The diseases are not the same, consequently the causes in each instance may differ. The rows, however, were not near each other and the conditions of infection may have varied. The green plants, as well as the spotted individuals in the second mentioned row, were but very slightly infected with *Puccinia sorghi,* which was the principal disease of the first case.

LEAF COLOR.

Among leaf colors in corn may be mentioned:—dark green, light green, red tinge, dark red, and variegated (stripes of white, yellowish green, and red). In varieties with green leaves occasional striped individuals occur, about the behavior of which little is known. Pure albinos which perish in the plantlet stage will not be considered under the head of leaf color.

Green.

Distinct shades of green are affected somewhat by humidity and plant food. The $\times_1$ hybrid from dark and light green parents were dark green when growing in the same soil and season (1910) with the parent varieties. It is possible that the dark green of the hybrid may be partly due to vigor of growth, but segregation of dark and light greens is to be looked for in the $\times_2$ generation. Price and Drinkard 69) also found the green leaf dominant to the yellowish green leaf in tomatoes.

Red Tinge.

Many varieties show a more or less red tinge on the leaf sheaths and edges of the leaf blade; this, in general, is associated with a red tinge on other parts of the plant, especially the culm, husks, and tassel. $\times_1$ hybrids frequently show this red tinge intensified where one of the parents has exhibited the character. $\times_2$ plantlets of two such hybrids were grown in the laboratory and gave the following results with respect to this character:—

Ear number.	Stems red.	Stems green.	Percent green.	Total No. of plantlets.
23.170×S.	10	3	23	13
36.205×S.	16	8	33	24

These numbers are too small to be of much value, but since large numbers of $\times_1$ plants growing in the field showed uniformly red tinge stems in hybrids of green and red tinge, we place confidence in the above results, and in more complete studies would expect perfect segregation of green and red tinge stems. Webber 85) found this red tinge stem appearing in mature plants of the first generation hybrids of Hickory King (green stem) and Cuzco ("purplish base").

Red coloring matter in many plants has been generally ascribed to "anthocyan"; which very general name for a series of red, blue, and violet coloring substances is usually the first and last resort in papers dealing with behavior of certain colors in plants. A large and interesting field awaits the student in this very important branch of heredity. In general, the theory prevails that anthocyans are produced from glucosides by oxidation, etc. Similarly to chlorophyll, anthocyans depend upon sunlight for their production and perhaps, in some cases, prevent the decomposition of chlorophyll by very strong light 64). It was noticed that bagging shoots retarded the production of red in the silks and on the husks which were covered by the paper bags.

Anthocyans occur in the cell sap of many plants and are soluble in water, the red tissues frequently giving an acid reaction. Transpiration is reported to be less

in red leaves than in green, and this character might be used to advantage in developing a drought resistant variety. When a leaf or stem is broken on the corn plant during the growing season, especially during the latter part of the season, the ruptured and surrounding tissue on the living end develops a tinge of red. This was noticed on many plants after the violent storm in 1910 and the color was apparently caused by oxidation of the cell sap. Blaringhem 9) secured a considerable amount of red foilage presumably as a direct result of mutilation and cutting of the main culm.

Dark Red.

Some varieties are of a deep blood red throughout the plant, others are only partly so in the husk, cob, seed coat, another, or silk color. Körnicke 51) noted a variety from Peru with blood red leaves and stem. Sturtevant 80) mentions receiving red-husked ears from the San Padro Indians of Mexico in 1886, a red-husked dent was advertised in 1885, a sweet variety with red stalks in 1889, and a pop corn with red stalks in 1895, but the history of their origin is not given. Frequently the new varieties introduced are from new combinations in hybrids and it is probable that some of the above varieties originated in this way. Halsted 36) noted the deep purple foilage of Ruby Sweet as dominant to the green foilage of a flint variety.

Only one hybrid (green foilage $\times$ dark red) was secured in 1909 in which the dark red foliage of one of the parents was constant, but of the kernels planted, only two grew. These $\times_1$ plants were very dark red throughout with the exception of kernel and cob colors. The endosperms were yellow and white, while the cobs of one plant were white and the seed coat colorless. These two plants were the most striking in the field because of their deep red foilage and perfect color segregation would be expected from their progeny.

Variegated Foilage.

Variegation occurs in some form in most families of flowering plants. In many species this phenomenon does not appear to be constant. DeVries 83) gives a large list of such instances and concludes that selection of variegated plants will not of itself lead to constant forms. Occasional striped individuals occur in corn as in all the Gramineae. So far as known all the groups of corn are subject to it. Sturtevant 80) mentions finding them in flint, dent, and sweet varieties. In our own work we found occasional striped plants in two dent varieties, one selfed pop, and two dent hybrids. These plants were selfed, closed, and hybridized but the $\times_1$ progeny have not yet been grown. The cause of the stripes is not known, but in some cases, they are associated with degeneration or abnormalities. Correns 20) and Baur 4) report several types of variegation in other species which (apparently) do not reproduce strictly true to seed, and consequently gave irregular segregation in the hybrids. Baur 5) found a case of yellowish green variegation in *Antirrhinum majus* which was always heterozygous, segregating into one-fourth clear yellow incapable of forming pigment, one-fourth pure green, which were constant, and the remaining two-fourths of the heterozygote form.

The first mention of constant striped varieties in corn, in so far as is known, was in 1861 and in 1866 33). These were said to have been brought from Japan and named "Japanese Striped" but the origin of the constant forms is not reported. Bailey 1) hybridized Zea Canina with Zea Japonica and in 1892 reported twelve green plants out of fourteen which indicates dominance of the green. The occurrence of the two striped plants may have been due to accidental self-pollenation. Variegated individuals of these Japanese Striped varieties, when selfed or closed in 1909, reproduced constant in 1910 without an exception. That the purity of these

varieties is to be questioned is evidenced by the fact that green plants were occasionally to be found coming from a mixed lot of the parent seed. The striping seems to be influenced by environment somewhat, more or less stripe appearing under varying conditions, thus we find variations in the stripping from almost pure green to almost pure albino. There is considerable fluctuation upon one plant and suckers are frequently found having more stripe than the main culm. In plants grown from hand-pollenated ears it was found that there were three types of the striping, namely:—More white than either yellow or red, more yellow than either white or red, more red than either white or yellow. It is not known whether these three types will behave as units.

Without exception, all $\times_1$ hybrids of striped and green plants, including twenty-seven cases and a large number of individuals, were green. This shows complete dominance of green foilage. The striped varieties, however, tend to have red tinge stems and leaf sheaths and, since this is a dominant character, when striped plants—having the red tinge in addition—are hybridized with pure green plants, the $\times_1$ progeny show the red tinge stem. There may be some variegated strains which do not have red tinge stems but in case none such are found, the above results might serve as an instance of broken correlation between two characters on hybridization, one being a recessive, the other a dominant and variable character. Whether there is an association of these characters in the $\times_2$ segregates is not known.

PUBESCENCE.

Individual plants in a number of varieties have a more or less heavy pubescence on the leaf blades. Other plants were found which were perfectly glabrous. The leaf sheaths of some of the rice pops have a dense, coarse pubescence. The data secured, indicates that pubescence in hybrids is a dominant character. Ten different $\times_1$ rows which were hybrids between varieties relatively smooth and varieties pubescent were especially striking for their dense, coarse pubescence on the leaf blades.

Dominance of hairs and spines has been reported in wheat, campion, stocks, and thornapple 3). Miss Saunders 3) found a very interesting case of correlation of purple sap color and hoariness in stocks.

The value of pubescence on the corn plant is not definitely known, although it is probable that this character would be desirable in a dry region. Collins 18) noted a Mexican drought resistant variety on which the leaf sheaths were densely covered with long hairs borne on tubercles.

CULM.

The diameter of the culm in Gramineae, as in most monocotyledons, increases by the enlargement of the cells of the young plant and not by the addition of new tissue, as in the cambium of dicotyledons. No study of the internal structure of culms was made but we might expect, from what is known of the method of enlargement of the stem, that there would be considerable constancy in the cross section of plants of the same strain.

There are two regions on the average corn stalk where most of the breaks occur by strong winds. One common break occurs at from one to three nodes above the soil, the other at the first above the earbearing node. Occasionally the break occurs at a node below the ear. Of these breaks, the most objectionable is at the base of the culm. Nearly all breaks occur on the upper border of nodes and not along the internodes; this may be explained by the fact that at the time of the summer storms the upper parts of the nodes are yet succulent and spongy, consequently they break quite easily. Every farmer who has cultivated tall corn early

in the morning knows from experience that corn plants break off much more readily at this time than later in the heat of the day when there is less moisture in the stem.

It would appear that in order to prevent loss from broken stalks the breeder should select individuals with firm, tough lower nodes, and large relative diameter of stem at this point in addition to a strong root system to prevent lodging and "down corn". Just such characters as have been mentioned, occur in different varieties, and unless correlations interfere, they are probably available by means of selection or by hybridization with individuals having other desirable characters.

When varieties or strains are planted side by side, the growing periods and relative stage of development must also be taken into account in comparing the effect of any particular storm or season. A stalk which is nearly mature is able to withstand a storm far better than one which is yet green and brittle.

A large proportion of the plants in several rows, some of them hybrids, were broken off near the soil in the season of 1910. These plants were usually slender and had a brittle appearance. Other rows also, including hybrids, tended to break above the upper shoot or ear. Plants and entire rows which lodged, and especially those which failed to straighten up afterwards, were those with slender stems and long internodes; therefore, not all slender stemmed varieties tend to break. No measurements of diameter of culms were made but, as was to be seen readily by inspection, there is a wide difference in this regard.

The product of coarse culm $\times$ slender culm and the reciprocal gave $\times_1$ hybrids with coarse, rigid culms. Slender culm $\times$ slender culm gave only a slight, if any, increase in diameter; which may be attributed to increased vigor. It is therefore apparent that the coarse culm is dominant to the slender culm in the $\times_1$ generation. It was noticed that the coarse, stout culms were characterized by thickened cortex and pericycle layers, but what relation the internal structure and the nature of the vascular bundles may have to strength of stem was not determined.

During the season of 1909, an abnormally large stalk was found in a field of pure-bred Leaming corn belonging to Mr. F. I. Mann of Gilman, Illinois. While the culm was yet green, it measured approximately two and one-half inches in diameter at the third node above the soil. An external examination revealed no other abnormality nor disease. Seed from the open-pollenated ear borne on this stalk was planted at the Illinois Station in 1910 and of the plants produced on medium soil, none measured more than an inch and a half in diameter. This shows that this peculiarity cannot have been a dominant characteristic at least, and evidently is not a genetic character since largeness in general is probably a Mendelian dominant.

"Vigor of plant as shown by ability to stand upright is hereditary. Ear-rows [dent varieties] growing side by side have shown a variation of from no broken plants to 56 per cent of broken plants—The ability to stand upright did not result from a lighter load" 87) Webber 85) noted much taller and thicker stems in $\times_1$ plants from Hickory King, a slender-stalked dent variety, pollenated with giant Cuzco.

HEIGHT OF PLANTS.

The response of the corn plant to food and environment is most significant in height and size, and for this reason alone there is always a possibility of finding considerable fluctuation in a study of these characters. Varieties are reported 80) to vary in height from 18 inches for a "Tom Thumb" pop to 30 feet or more for varieties grown in the tropics. Undoubtedly many of the difficulties which have been experienced in interpreting the behavior of size or length of parts may be attributed at once to abnormal environment and to impurity of strains.

In his original paper on hybridization Mendel 58) reported complete dominance, in fact, increase in height of sweet pea plants, followed by complete segregation. "The longer of the two parental stems is usually exceeded by the hybrid, a fact which is possibly only attributable to the greater luxuriance which appears in all parts of plants when stems of very different lengths are crossed." He secured a ratio of 2.84 talls to one dwarf in the next generation with 1064 plants. McCluer 57) hybridized two varieties of pop corn and secured plants taller than an average size of the two. Hartley 40) states that a hybrid of Mexican Dent corns produced plants 2¾ feet taller than the average height of the tallest parent and 4¾ feet above the average of the shortest parent.

Tschermak 3) reported apparent inconstancy with regard to height in bean hybrids. DeVries 83) found that extracted F_2 dwarf antirrhinum did not breed true, but gave progeny of various heights. In a hybrid of giant Cuzco and Hickory King dent corns, Webber 85) noted that the $\times_1$ generation was much taller than either parent. The Cuzco had been stunted, however, by being started in pots and then transplanted. Hybrids of Turkey Red wheat with Russian Winter were reported by Keyser 50) to have made a height growth fully 10 inches greater than either parent.

Lock 53) working with corn concluded that the height of $\times_1$ hybrids "was obviously intermediate—In a number of cases the cross was made between the F_1 plants and the shorter of the parental types. The offspring of this cross showed no such segregation into short and intermediate plants, as was to be expected if Mendel's Law held good." Price and Drinkard 69) found "standard stature" (tall) dominant to "dwarf stature" in tomatoes, giving complete segregation in the $\times_2$ generation. As a result of his observations on measurements with hybrid rabbits and guinea pigs, Castle 14) proposed that "Size variation is apparently continuous and its inheritance blending—[but]—Blended inheritance may possibly be only a complex sort of Mendelian inheritance, in which many independent factors are simultaneously concerned."

Emmerson 29) stated that in every case with which he is acquainted, there has been segregation of size characters in $\times_2$ following the blend in the $\times_1$ generation. Crossing a Tom Thumb pop 90 cm in height with a late dent 225 cm in height: Emmerson secured approximate blending with regard to height (182 cm), number of nodes, and growing period. He found $\times_2$ plants ranging in size from the Tom Thumb to above that of the $\times_1$ generation but none were as tall as the large dent parent. East 28) secured $\times_1$ plants from a medium sized flint and a tall dent which were nearly equal in height to the tall dent parent. East attributes the increase in size of the $\times_1$ plants over the average of the two parents to increased vigor as a result of hybridizing and not to dominance of tallness. The distribution of heights in the $\times_2$ generation was more variable and no definite segregation was apparent other than this difference in fluctuation between the $\times_1$ and $\times_2$ generations. He concluded that a combination of many characters may be necessary to produce size.

Thus, in general, the disposal of size-inheritance has been unsatisfactory. In the first place a size somewhere between the heights of the parents, represents no actual increase, although it is above the average of the two. Practically we would not concede an increase unless we secured a hybrid larger or taller than anything we used to produce that hybrid. This complication due to vigor may perhaps never be overcome, but we need at least an approximate method of evaluating its influence before we can say how size segregates.

Undoubtedly a system of height classification based only upon inches or centimeters is unsound. It is hardly rational to expect corn plants to vary in units of the yard stick or bushel measures, and to attempt an analysis of inheritance from this viewpoint alone, or to expect "bushels per acre" to segregate, is extremely

fallacious. Perhaps the division into dwarfs, intermediates, and giants is as far as we may go at present with our limited knowledge of what constitutes height. If it is not possible to find characters correlated with height, it will be necessary; as Bateson, Castle, and others have recognized, to determine the units—of which there are probably a number—that together control size.

In general, the $\times_1$ generation was more uniform than the parents; which is especially true of the selfs and closes. The arrays were made in five-inch classes since the error in finding the height of a plant of this nature can scarcely be limited to one inch.

In my work the fluctuation in the parent rows in 1910 was generally less than in the poorer soil and season of 1909. This accords with the conclusions of Davenport and Reitz 22) upon measurements and weights of ear corn. They report variability to be slightly less on fertile land than on lands giving lower yields. Love 64) has reported increased variation with increased food supply in height the number of internodes of garden peas. Humbert 44) found indications of a decrease in variation in night flowering catchfly with an increase of plant food in the soil.

In general the $\times_1$ generation is more uniform than the parents, which is especially true of selfs and closes; this accords with observations by other investigators and is explained, partially at least, by the fact that the immediate parantage is restricted to two individuals in the case of hybrids, crosses and closes and to one parent in the selfs. For practical purposes the stragglers or poorly developed plants in such cases as; 15.100, 22.129, 25.170 etc. may be neglected.

While Gregor Mendel 58) stated in his paper on hybrid peas; "It is furthermore shown by the whole of the experiments that it is perfectly immaterial whether the dominant character belongs to the seed-bearer or to the pollen-parent; the form of the hybrid remains identical in both cases"; a number of instances have since been observed where this principal does not seem to hold. Bateson 3) has proposed two possible explanations of "the remarkable fact that the mother-plant can impress varietal characters on her offspring by influences which are not hereditary in the ordinary sense", namely,—the difference in food materials in the seed, and the presence of a specific factor or factors.

From a large number of observations on plant and seed characters in corn, we feel that either or both of these explanations may be justified in the same individual. A summary of the reciprocals in regard to height given in Table 3 exhibits general uniformity in results:—

No.	Reciprocal Hybrids. Modal height in inches.	No. of plants.
210×404	110	36
404×210	120	4
304×503	45	47
304×503	50	49
503×304	45	30
310×408	125	16
408×310	125	28
502×610	105	13
610×502	105	19

With the exception of the 404×210 hybrid which produced only four plants, the results may be considered as uniform. In numerous cases—not reciprocals—it was noticed that where dent corn was used as the female parent, taller and coarser

stalks resulted than when it was used as the male parent on the smaller sweet, flint, and pop varieties; while this difference is noticeable in the mature plants, it is especially striking in the plantlet stage as has been mentioned. Reciprocals made in 1910 between rice pop and large dent varieties exhibited a wide difference when growing side by side in the $\times_1$ plantlet stage in the laboratory tests. In some of these instances, at least, the difference seemed to be due to unlike food material in the kernel,—unlike it seems, in both quantity and quality.

Thus it is apparent that differences in vigor and size exhibited in seedlings may be noticeable in the same plants when mature. It may be that the explanation of increased vigor of hybrids depends largely upon this one fact—vigor of seedling—due to the quantity and composition of food material in the germinating seed, which favors an initial, vigorous cellular—activity upon which luxurious development depends.

The modal summary of the behavior of height shows some very interesting results with variations from what appear to be increases in height to those cases which appear to be perfect blends and others that seem to be decreases below the height of the shorter parent. Twenty-three cases out of forty-five possible ones in the $\times_1$ hybrids gave modal heights greater than either parent individuals and modes. In five cases $\times_1$ hybrid modes were below the parent, individuals and modes. How these hybrids would behave in the $\times_2$ generation would make a very fascinating study indeed. The closes gave variable results, as is to be expected in view of the unknown purity in the seed. With regard to height, there may have been as wide difference in the majority of individuals used in the production of hybrids. Had "pure" strains of corn been available, we would have expected a decrease in height in the majority of $\times_1$ closes. Some of the increases in height observed in the $\times_1$ closes may have been due to acclimatization; again, we may have had a wide difference in the individual parents of some of the closed cases.

From the experience of McCluer, Shull, East, and others, we would expect all the selfs to appear in the column, "Below the Lesser Parent", ie; decrease in vigor the first season because of self-breeding. To our surprise, we find one case giving $\times_1$ progeny as tall as the parents (Equal to the Average of the Parents) and another taller than the parents (Above the greater Parent). In the case of increase (2S.170) there were only nine plants but confidence is placed in their behavior, although the parent mode chosen may not have been exactly correct because of the limited array given. The hybrid kernels from this same ear (23.170) gave plants taller than the selfed individuals although the 309 variety averaged somewhat shorter than the 210 variety. It is suggestive that these two varieties, both popcorns (201 and 210) may permit inbreeding for a time without serious loss of vigor. The two closed populations (2C.163 and 2C.164) of 210 gave further evidence in favor of this conclusion.

INTERNODES.

The question arises as to what hereditary factors determine height and, as a matter of course, it is to be expected that the number of internodes and their relative length would determine mere linear dimension. It is also surmised that number of internodes, within a variety, is a more constant quantity than either height or average length of internodes.

The possibility of correlation of number of internodes with yield or production and with some other characteristics has been investigated, but so far as known, no correlation tables have been constructed between number of internodes and height of plant. Ewing 31) found the coefficient of variation for number of internodes within one variety of corn to be less than for a number of other plant characters studied. The results in selection during six successive years as given by Smith 76) give evidence of a direct correlation between height and number of

internodes within each of the two strains, "high ear" and "low ear". In the data given by Smith, the number of internodes is plainly more constant than their average length. Certain varieties exist, however, in which the average length of internodes remains quite constant.

Cases of "telescoping" or shortening of internodes have been found to reproduce. Hartley 39) describes stalks 4 to 5 feet tall bearing 18 to 20 broad leaves in a white dent variety whose normal height was 10 feet. These short plants were pollenated with each other and the dwarf character was reproduced by their progeny.

In the season of 1910 in a plot of Leaming, a tall dent corn, here at the Illinois station, a stalk was found having 17 internodes, probably the average of the variety. This plant was only 37 inches in height while the average of the plot was approximately 120 inches, and the largest leaves of this plant were as long as the culm of the plant itself. This average length of internode of slightly over two inches as against approximately 7 inches in the normal plants presented a very dense-leafed effect. No ear was produced on this plant but its pollen was used on two other strains of Leaming corn with success. As short internodes is expected to be recessive, if there is an inheritance of the peculiarity, it cannot appear till the $\times_2$ generation has been grown.

With a given height, extreme length of internode is not desirable unless it is accompanied with a large diameter of culm and a well developed root system. Extremely short internodes are also undesirable, as such varieties usually produce short leaves and small ears, with a corresponding decrease in other parts of the plant. In general, the length of internode on a corn plant is least at the roots, and increases toward the tassel and, in many varieties, there is again a decrease in length of internode between the upper ear and the tassel.

In Emmerson's 29) Tom Thumb Pop$\times$Late Dent hybrid, an intermediate number of nodes (8 nodes$\times$19 nodes gave 12 nodes in the $\times_1$) was obtained in the $\times_1$ generation, but segregation was predicted for the $\times_2$ generation. Assuming that the number of nodes given by Emmerson corresponds to the number of internodes, we interpret his results as follows:—

	Height of plant.	No. of internodes.	Av. length of internodes (Including the tassel).
Tom Thumb...........	90 cm.	8	11.3 cm.
Late Dent.............	225 cm.	19	11.9 cm.
$\times_1$ Hybrid.............	182 cm	12	15.2 cm.

While he secured a gain of 3.3 cm. in average length of internode, his $\times_1$ plants showed a decrease of 7 internodes as compared to the taller parent. This behavior indicates either dominance of small number of internodes, or that one or both the individual parents used were heterozygote with respect to number of internodes; unless number of internodes can be shown to actually blend.

Because of the very short internodes at the base of the plant, some of which may be covered in cultivation, it is impracticable in most cases to secure a count of the total number with an experimental error less than 2 internodes.

It is practically impossible to get the exact number of internodes at the time of maturity of the plant without dissecting the rooted portion of the stem. Carefully marking the sixth or seventh leaf of the young plantlet while the coleoptile or plumule sheath is yet discernable and which is borne at the first true node, would be, perhaps, the most satisfactory and definite method of counting internodes.

In the behavior of the hybrids it is significant that height of plant is affected more frequently by difference in average length than by difference in number of internodes. It was found that closing and selfing gave a decrease in average length but no significant decrease in number of internodes.

Among the hybrids there were a number of cases which fluctuated considerably from the modes of the parent strains, and the modal summary shows very clearly that the fluctuation in results is largely due to hereditary differences in the individual parents. The summaries show at a glance that both large number and greater average length of internodes predominate in the $\times_1$ hybrids, the majority of cases falling in the lists "Equal to and Above the greater Parent". Closing and selfing seems not to have any decided effect upon the number of internodes, while there was a decrease in average length in the majority of cases.

From the results obtained, it is evident that more reliable data and greater accuracy in interpretation may be expected with regard to number of internodes and their relative length than from observations on mere height of plant in units of measure. These two characters do not behave alike in all cases in transmission, and do not seem to be correlated. Decrease in average length of internode seems to be the principal cause, at least in the first season, for "decrease in vigor due to inbreeding" in so far as height of plant is concerned.

AERIAL ROOTS.

After the secondary roots, which develop at the first few nodes on the stem, have become established, the primary root is of very little importance and later ceases to function, as is characteristic of monocotyledonous plants.

The first few whorls of secondary roots are usually very close together, making it difficult to distinguish the internodes. Succeeding whorls of aerial roots, commonly known as "brace roots", frequently develop at a considerable height on the culm from which they can no longer reach the soil, unless the plant is bent or lodged; in that case the aerial roots always start from the side of the node nearest the soil, sending out a mass of fibrous roots after penetrating the soil surface, thus anchoring the plant firmly in its new position.

The aerial roots are forced through the epidermis of the nodes. They are usually quite fleshy, and have a gummy surface which is said to be due to the breaking down of the outer cell walls. During a rain or when immersed in water the gum accummulates at the root tips as a transparent jelly-like mass. This gelatinous substance is tasteless and gives a neutral reaction with litmus. The gum prevents dessication and affords protection for the tender surface of the developing roots.

Some varieties have the aerial-root character well developed while others do not show it at all. So far as known no selection for these roots has been reported. The character is fluctuating in its behavior, being affected by environment and vigor. Border plants frequently produce the roots higher on the culm than do plants in the center of the plot or field. One plant of large Mexican corn (408) on the end of a row in 1909 produced aerial roots at the thirteenth node above the soil.

Counts of the aerial root whorls were made only in 1910. The fact that very few of the $\times_1$ generation and only a limited number of the parents produced plants with only "one rooted node" above the soil, favors the conclusion that when varieties produce aerial roots at all, they tend to do so on several nodes. Certain strains produced no aerial roots which failed to reach the soil. In the large majority of the $\times_1$ hybrids, a high number of rooted nodes predominates, when this feature was found in one of the parents. Closing gave variable results depending on the parentage. In the selfs the number of nodes with aerial roots decreased in three out of four cases observed.

PERIOD OF GROWTH.

The origin of varieties with very short, and others with extended growing periods has not been recorded, but varieties exist that are adapted to regions

differing widely in soil and climatic conditions. Considerable local adjustment may take place in a few seasons in varieties whose requirements are not adapted to the new conditions in which they may be placed. Sturtevant 80) recorded differences in growing periods of from one to seven months in varieties growing in different regions.

After five years of selection for high and low ears, Smith 76) observed that the "low-ear" plot was apparently a week in advance of the "high-ear" plot at the tasseling stage. The low ear character is associated with a decrease in height of stalk, shorter internodes, and a decrease in number of internodes below the ear.

Pearl and Surface 67), after three years of experience in selecting sweet corn, report; "Many of our results seem to indicate that earliness, in a large part at least, is a physiological rather than an hereditary phenomenon—all the gain which has been made in earliness was accomplished in the first year's selection. No further increase has followed the further selection practised in the two subsequent years."

Emmerson 78) has found apparently little correlation between height and earliness in the second hybrid generation of two varieties of corn, some of the earliest plants being above medium height and some of the latest being very short. He reported the $\times_1$ generation as intermediate in maturity (100 days) between parents whose growing periods were approximately 70 and 130 days respectively. Mendel 58) failed to complete his report on the study of this character in peas, but found that the first hybrid generation was intermediate and predicted segregation if hybrids were made in which the parents differed at least twenty days in maturity. Biffen 8) also noted intermediate results with hybrids of early and late wheat varieties.

In our study of this question, the "period of growth" will be designated as the time in days between the planting of the seed and the date upon which the husks on the upper ear or shoot are dead. We do not assume that growth in the plant as a whole ceases definitely at this stage, but the time at which all green has disappeared from outside husks provides perhaps as definite and satisfactory a point as can be secured for comparison in regard to the total growing period. After this stage in ripening, there is undoubtedly considerable deposition of substance in the ear and in other parts of the plant in some cases. Incidentally it was noted that some varieties ripen their husks a number of days before the remainder of the plant matures. The period of growth may properly be divided into two stages by the date on which the silks of the upper shoots on most of the plants appear. This point in the blooming period was taken because it is the time when the process of reproduction begins.

Notes were taken daily on each plant in 1909 on the appearance and character of the tassel, anthers, and silks, and it was found in a number of instances that the relative time of the appearance of these three was quite irregular. Since the planting was done at three different times in the first season, only data from 1910 were used for comparison with the $\times_1$ generation. This data was taken every four days on the appearance of anthers and silks only. The differences in length of blooming periods are frequently due to poorly developed and abnormal plants, yet some varieties pass the period very quickly (10 days) while others have a very extended period (20 days or more). In general the blooming period of the $\times_1$ hybrids tends to be longer than the average of the parents. Eleven hybrids in the list of those observed had a period equal to or less than that of the parent with the shortest period, while sixteen other hybrids had a period equal to or longer than the average of the parents: nine being equal to or longer than that of the parent with the longest blooming period. Among the closed cases, six out of nine required more time to finish blooming than did the parent rows in the same

season. Two of the three selfed cases had blooming periods identical to those of the parents and No. 201 (selfed) finished blooming in a much shorter time than its parent.

While protandry is the most common behavior in floral development in corn, no very extended observations on the inflorescence at the time of blooming are necessary to bring to notice individuals which do not shed pollen till some time after the silks appear. As examples of differences among the varieties, No. 203 had eighteen plants which showed silks on a given date while only five among that number were as yet producing pollen. When this variety was closed and hybridized the progeny gave a normal behavior. Other varieties, notably 503, 603, and 610 produced no silks until approximately eight days after the first anthers appeared. It is striking that a somewhat similar behavior prevails in the closes and selfs of 503 and 603.

The reciprocals differed somewhat in time of appearance of silks after planting. This difference varies from four to eight days, and may have some significance, but the general result is the same; that is, the longer periods tend to be dominant in the X_1 hybrids. The hybrid 24.162 was approximately a week later in blooming than its reciprocal 42.238. It may be that the difference in location in the field may have had an influence, but it was more probably due to the difference in the individuality of the parents on the 210 side. This is also another example of difference in behavior when dents are hybridized with smaller varieties. The large dent kernels of 42.238 should give the plantlets an initial advantage over the plantlets from the very small kernels of 24.162. Close and self pollenation delayed the time of blooming in the majority of the X_1 progeny. While the results do not permit definite conclusions to be drawn, the balance is decidedly in favor of "late blooming as being the dominant character."

A partial list of the total growing periods varied, in the parent strains used, from approximately 100 days to nearly or perhaps fully twice that length of time. This table also showed the number of days in the latter part of the growing period. The uniformity of this latter period in comparison with the total period is significant in all those cases in which maturity was reached. The exact average fraction of the total time for both the parents and the X_1 generation is 0.39 or approximately 0.40.

If this fraction were constant for all the varieties and their progeny, it would afford a ready means of calculating the total growing period when the time from planting till silking is known; and thus provide a method for learning the total growing period in those cases which did not mature because of the short growing season. There were, however, extreme fluctuations of from 0.31 to 0.45 and there must have been similar fluctuations in the varieties which did not ripen. In testing this proposition on some cases which did not mature, by adding 40 percent of the total (equal to ⅔ of the time from planting till the appearance of the silks) to the number of days from planting till the silks appeared, a few of the cases should have been ripe although they are not so shown in the field data. While further and more conclusive tests of the relative lengths of the two periods of growth are necessary, the results secured indicate that approximately 60 per cent of the total growing period in corn preceeds the time of the appearance of the silks; the remaining 40 per cent of the total growing period falls between the time of silking and the time when the husks on the ear are dead.

The data are too incomplete for a summary. In a number of cases, the X_1 hybrids ripened late or failed to ripen at all. There is sufficient evidence of this nature in the tables to permit the conclusion that late maturing is dominant to early maturity. Since the total growing period tends to be longer in the X_1 hybrids than that of their earliest parents, the period between silking and time of ripe husks is as a consequence also longer.

There are numerous indications that the present monecious type of inflorescence in corn has developed from a terminal hermaphrodite form. Hackel 34), Harshberger 38), and others have recognized the origin of the ear of corn, as we have it now, as due to a union of two rowed spikelets of the floral clusters on the tillers or plant branches. Harshberger has pointed out further that clusters of these fasciations or ears probably existed in the primitive form, and "one ear, in the cultivation of corn for centuries, has enlarged at the expense of the others, furnishing another illustration of the law of compensation in growth." These ear clusters mentioned by Harshberger are of common occurrence in many varieties today, being found in the terminal inflorescence of suckers and also upon the shanks and among the husks of ears on the primary culm. Sturtevant 80) mentions the frequent occurrence of such cases.

Montgomery 59) proposed that the ear has developed directly from the central spike of the tassel without fasciation, the lateral branches of the tassel disappearing as a consequence. It is a well known fact, however, that the large majority of ears in many varieties are "spread", that is,—larger in one diameter than in the one taken at right angles to the first. (The frequent occurrence of such ears indicates that it is a dominant character.) Quite frequently, also, ears with enormously spread or fasciated tips are found, and such features are very strong evidence in favor of the fasciation theory. The fact that large husks (not enlarged glumes) are frequently found in among the kernels near the base of the ear also the occurrence of kernel baring branches not only at the base of the ear but at some distance above the base of the ear are further evidences in favor of the same theory. The recurrence of these branches indicates that they were absorbed but not lost.

A very interesting case arising in our own work offers evidence in favor of the fasciation idea rather than the theory presented by Montgomery. In harvesting one of the Illinois Experiment Station plots, the men found a peculiar cone-shaped ear with a prolificated cob. A section of the ear disclosed only a large central pithy core to which were attached the slender branches. The kernels (borne in pairs) and glumes were irregular in size and shape (due to the irregular distribution) but normal otherwise. Fifty plants were grown from this ear in 1910 and two of that number bore exact duplicates of the mother ear; this fact indicates that the prolification is a character and will reproduce. The pollen on these two plants grown in 1910 was nearly all gone before the silks developed; it is probable that the mother plant behaved similarly and that the seed was largely cross pollenated by normal plants.

If this behavior, which appears to be a reversion, is a recessive character, it would account for the small number of individuals which reproduced the prolification. One of the ears was pollenated by a normal individual in the row and in case this character behaves as a true recessive, the $\times_2$ generation of the hand pollenated ear should produce fifty per cent of proliferous cobs. The peculiar ear character is associated with a distinct tassel type, which is also cone-shaped, bearing numerous short branches. Advantage may be taken of this fact in the selection of such individuals before the silks appear.

Historical investigations indicate that the number of rows on the primitive type of ear was not very large, probably ranging in number of rows from four to fourteen, and in some varieties there has since been a decided increase in size and number of parts in the ear as well as in other parts of the plant. It is evident that large proportions within paired spikes or rows in the cob are responsible for large, broad kernels. This enlargement of parts, including kernels, appears to have taken place at the expense of other parts, such as anthers and glumes, as well as of one

of the entire florets of the original pair (Embryonic kernels are paired in the row similarly to the pairing of the rows themselves, but the lower flowers in each spikelet are generally abortive) 80). This increase in size of the female parts seems also to have been associated with decrease in the leaf blade and telescoping of the internodes on the ear bearing shank.

In regard to the origin of the ear-bearing branch Montgomery suggests that as evolution progressed, the central tassel came to produce only staminate flowers, the pistillate ears being produced on the tiller-like branches, which became shortened until the leaf sheaths enclosed the ear.

Blaringhem 9) found a close correlation between the length of the supporting stem and the type of terminal inflorescence on suckers; those having only female flowers being borne on the shortest stems while those bearing a mixed inflorescence were borne on longer stems. It is well known that extremely large pods in the pod corns may develop not only at the expense of the cob, but of the entire floral parts including the kernel. Pod corn frequently develops a large amount of grain or very heavy glumes in the tassel, in which case it often happens that no ear develops on the culm.

When a number of rows of kernels are combined in the central tassel spike, there is a thickening of parts and in most cases a decrease in the number of branches.

Development of scattered, medium sized, rounded kernels are frequent in tassels which show no perceptible thickening or enlarging of tassel parts. This behavior is very common among pod corns and tends to reproduce. Sturtevant 80) reported slight or no indication of the transmissal of this character from wind-pollenated seed. He also noted hermaphrodite flowers and staminate clusters on the cobs of other species groups. Blaringhem 9) secured hermaphrodite ears from mutilated flint corn parents and reports the second generation as being constant in the production of anthers on the ear. Montgomery 60) has recently reported finding perfect flowers in well developed ears. In our own work, a number of similar cases have been found, but of their inheritance we know nothing except in the case of the pod corn. In this study no instance was found (in a large number of cases observed) where both floral parts functioned in the same flower either in the tassel or on the cob, although both anther and pistil are present; one always functions at the expense of the other which is poorly developed, thus insuring pollenation between florets at least. In the season of 1910, an abnormal plant was found which bore two medium sized ears, but no indication of a tassel.

Cases of barrenness or complete sterility will be discussed in connection with the paragraphs on "Pollen" and "Shoots".

TASSELS.

Aside from notes on hermaphroditism and abnormalities, there are but few reports upon tassel characters. Various investigators have noted differences in the number of tassel branches. Collins 18) noted frequent cases in a Mexican drought resistant variety in which the tassels were unbranched and the normal form itself produced but few branches. Shull 75) reports an apparent decrease in the number of tassel branches in a self-bred strain. Webber 86) found a correlation between the kernel color in Black Mexican sweet corn and green tassel glums and anthers. This correlation was but rarely broken.

Structure.

Styles and sizes in tassel structures are various and, in our own work at least a dozen distinct types or forms have been found. No one tassel was found which

possessed all the dominant units, consequently the various hybrids gave many new combinations not observed in the parents. To the casual observer these tassels of the $\times_1$ hybrid would apear a blends very analagous to the supposed blends in

Fig. 2.—Some distinct tassel types.

height of plant. The detection and sorting of the segregates with respect to certain tassel characters may prove as difficult an undertaking as that of determining the units which control height in the plant. It is evident that the twelve types chosen are themselves the combinations of many units.

In the $\times_1$ hybrids, we found the following tassel characters apparently dominant:—large size, long spike, erect spike, long branches, many branches, spreading branches, coarse parts, thick glumes, large glumes, monstrous glumes. On many of the $\times_1$ selfs and closes, we noticed a decrease in the number of branches on the tassel as was reported by Shull 75) on self-bred strains. It might be assumed that the behavior just mentioned is due to segregation, but a number of observations in our own work led to the conclusion that it is a decrease in vigor of branching. This is very similar to the decrease in the number of suckers observed on our self-breds and although Shull has not mentioned this fact his photographs show his "Strain A" which was originally suckered, as no longer producing them.

Color.

In varieties that were known to be fairly pure, and especially in self-breds, the tassel colors were fairly constant but in the majority of the varieties used considerable mixture existed in these characters. Red tinges in the tassel were shown to be dominant to green in a number of $\times_1$ hybrids. As has been mentioned in connection with colors of the culm and leaves, we were unable at the beginning of the study to secure a variety that was constant with respect to deep red color throughout. Dark red tassels are relatively numerous in some varieties and their frequent appearance in the $\times_1$ generation indicates that this is a dominant character.

Male Flowers.

The male florets in clusters of two or a multiple of two, one pediceled, the other sessile, or both sessile, are usually arranged alternately in the panicle. In the four varieties secured from Arizona an opposite arrangement of spikelets

occurs at many points in the tassel, similar to the behavior in a Mexican variety reported by Collins 18). Cases of paired spikelets were found in hybrids with these variations in 1910.

Differences in size and texture of glumes have been mentioned in connection with tassel types. Colors in the glumes behave similarly to those on the stem of the tassel, frequently, however, the glumes are colored when the tassel stems are not; quite often a distinct red ring is formed at the base of the florets in those varieties having red tinge tassels. "Red tinge" or "red base" in the glumes and their deeper colored form "reddish green" are dominant to pure greens. Dark red glumes from mixed parentage gave results which indicate dominance of that color over red tinges and pure greens.

ANTHERS.

The anthers in the floret of a corn tassel are usually three in number (sometimes four to six where doubling of parts occurs) and vary in different individuals and varieties as to size, shape, color, and fertility.

Size.

During the hand pollenating work of the two seasons, a small quantity of anthers was preserved from representative individuals in the parents and the $\times_1$ generation. These anthers were thoroughly dried in the tassel bags and samples stored in small glass vials for future reference. Among these cured anthers, distinct differences exist in regard to size and shape. Such differences had been observed in the field but since there was no opportunity for taking measurements, only general statements regarding their behavior can be made.

Extreme length is not always associated with large circumferences in anthers, and long anthers are not always found on tall growing varieties. Anthers below the average in length were found in some varieties, upon very tall plants. Long anthers were found in other varieties producing small plants. In the $\times_1$ hybrids, a number of cases were found where long anthers were dominant to short anthers. Many intermediate cases were found, which were attributed to distinct differences and heterozygosis in parents with respect to this character. No definite statement can be made in regard to the behavior of relative size and circumference in anthers, but differences exist in this respect as well as in length.

Color.

Carful notes were taken on the color of anthers upon every plant grown in 1909 and upon every plant hand pollenated or from which pollen was secured in 1910; thus exact data are at hand on the behavior of anther color. The color in dried specimens was preserved perfectly in most instances. A number of striking colors and beautiful tints were found. None of the varieties used were absolutely constant in anther color, consequently only a limited number of cases were found in the $\times_1$ generation in which the anthers were of the same color on all the plants of a population.

Among the many combinations made, we find cases as follows:—green (anthers) $\times$ green, giving only green; green $\times$ reddish green, giving only reddish green; and other cases giving colors from pure green, reddish green, to dark red; either green or reddish green $\times$ deep red giving all deep red and some giving mixed results from pure green to very dark red. From this it is evident that dark red—when homozygous—is dominant to other colors, while pure green is recessive to colored anthers (red tinge, reddish green, and red).

Increased uniformity was secured in another color in all the closes and selfs. This uniformity including that of glume colors was a striking feature in self-bred strains. One closed case (502×C) in which one parent had pure green anthers and the other reddish green, gave $\times_1$ progeny all having reddish green anthers. This case gave the same results in regard to another color as was secured in hybrids between varieties because—as is apparent—we closed a pure green with a pure and dominant reddish green segregate. The anther color of the majority of plants of the parent variety was green. This is another of the many instances of mixture of characters in a variety which is popularly said to be "pure".

Tests were made of the behavior of the light green anther which Webber 86) reported was correlated with kernel (aleurone) color in "Black Mexican" sweet corn. Two $\times_1$ hybrid populations of this variety with others having reddish green anthers gave $\times_1$ progeny all having reddish green. In Webber's own observations upon $\times_4$ segregates of a hybrid of this black sweet variety with one having reddish green anthers, he reports almost perfect correlation of the pure "black" or purple kernels with green glumes, anthers, and silks. If the correlation is not permanently broken, we should be able to pick out the $\times_2$ plants homozygote to the dominant kernel character—purple—by selecting those plants bearing green anthers. If such results can be secured in the $\times_2$ generation it will serve not only as an example of broken correlation in so far as its expression is concerned in the $\times_1$ generation, but also as an instance in which a homozygote dominant can be separated from the heterozygote dominants in the $\times_2$ generation because of the correlation of a dominant and a recessive character.

Among the Black Mexican plants growing in 1909, four out of 108 individuals produced red tinges on the anthers and silks. This may be due either to impurity or to imperfect correlation. Webber also found stray individuals in the $\times_4$ segregates exhibiting red tinge silks and glumes which he attributed to breaking of correlation by hybridization.

Sterility.

Kölreuter and Gärtner among other early investigators thought that sterility in hybrids was a means of distinguishing species. Darwin investigated many cases by which he was able to point out the fallacy of this belief. In an explanatory statement in connection with an instance of total sterility in corn, DeVries 82) concludes; "barrenness is to be considered as a monstrosity, which like all other monstrosities, is inherent in a race, but is developed only in a certain percentage of its individuals."

A number of instances of sterile anthers have been reported in inbred corn. From our knowledge of heredity gained since these cases were reported we know that they have been the result of using parents in which sterility existed, rather than sterility being the immediate result of inbreeding itself. Hartley 40) reported two hybrid cases in corn which showed a strong tendency toward sterility. Suckers developing adventitiously from mutilated plants were stated by Blaringhem 9) to have produced tassels with infertile stamens, but such a condition frequently exists on poorly developed suckers in corn.

In a hybrid of Maryland white dent and blue Hopi corn, Collins 18) found six out of sixteen plants which failed to produce pollen. Sterility has been reported in hybrids with other species than corn, but the behavior does not seem to be the same in all cases. Normal anthers are reported to be dominant to sterile anthers in sweet peas 3).

In two of the parent strains used in our experiments the majority of the tassels bore largely sterile anthers. A number of the plants produced a small quantity of pollen insufficient for our needs, others gave no indication of sterility. All the hybrids as well as the closes with these two strains gave, without exception,

X_1 progeny with partially or completely sterile anthers on the most of the plants. It is therefore expected that a careful analysis of this abnormality would show that it is a Mendelian dominant in corn. In many instances of total sterility, the flowers never opened while in others the hard shrunken anthers were discharged. These latter individuals were at first bagged, before we became aware of their nature, with the expectation of securing pollen. Such a character if it is dominant could of course not be transmitted unless it is pollenated by a homozygous recessive. This is another instance of a character, fatal in itself, depending on heerozygosis (in this case, pollen of a recessive on a pure or a heterozygote dominant) for its perpetuation. Thus the character, while it insures mixed-pollenation, is yet undesirable because it is a dominant one. Some individuals were found having a few fertile anthers among the many sterile ones in the same tassel.

POLLEN.

The daily field notes taken in the season of 1909 upon individual plants, recorded the exact time of the appearance of pollen and silks upon approximately 5000 plants representing a large range in varieties and all the species groups. A number of cases were noted in which the silks appeared on the upper shoot at from one to three days before any pollen was shed from the tassel of the same plant (protogyny). The large majority displayed a similar and frequently greater variation in the opposite direction—anthers before silks (protandry), while many instances were found in which the anthers and silks appeared on the same day (synacmy).

In the cases mentioned, we thus found a variation in the difference of time in days of from minus three to infinity, if we include those plants which produced no silks at all or were "barren" in so far as production of ears was concerned. We may therefore expect in many varieties, a normal fluctuation of from one to four or five days in the interval between the appearance of pollen and silk on the same plant. Several varietial differences in this respect have already been mentioned under "Period of Growth" (see page 80).

Sturtevant 78) made similar observations on single plants, noting first—blooming in each row of the different varieties grown and from his data we have compiled these results:—

Group	No. of rows.	No. of Varieties.	No. showing pollen before silks.	No. showing pollen and silk at same time.	No. showing silk before pollen.	Extremes in days.	Av. difference in days.
Dent	46	12	39	7		0 to 9	2.6
Flint	23	12	21	2		0 to 8	3.4
Sweet	49	27	39	8	2	—2 to 8	2.4
Soft	11	2	10	1		0 to 5	1.1
Pop (common)	8	4	7	1		0 to 7	3.5
Pop (pearl)	8	4	7	1		0 to 6	2.0
Pop (rice)	14	7	12	2		0 to 3	1.7

With the exception of being the first to bloom in each row, these plants were supposedly normal.

Lazenby 52) reported observations which extended over several years upon 15 or more distinct varieties, as follows:

PER CENT OF INDIVIDUALS SHEDDING POLLEN WHEN THE SILK APPEARED.

	Some pollen shed.	½ pollen shed.	All pollen shed.
Dent 6 varieties........................	95	76	32
Flint 4 varieties........................	89	60	38
Sweet 8 varieties........................	98	82	44

As in our own experience, Lazenby found that it is not always easy to tell just when the pollen is all discharged. With different tassels, we found the pollen production to extend over a period of from four to eight days.

In 1875 Sturtevant 77a) counted pollen grains in a large number of anthers, and the number of florets in the tassels. From his results Sturtevant concluded that the average number of pollen grains in an anther is 2500 and the number of stamens in a tassel 7200. Allowing two ears of 1000 kernels to each plant, there would be approximately 9000 pollen grains for every ovule to be fertilized. Using Sturtevant's estimate of 2500 pollen grains in an anther, Lazenby 52) computed the ratio of number of ovules to number of pollen grains by counting the flowers in several average sized panicles in dent, flint and sweet corn.

LAZENBY'S CALCULATIONS.

	No. of ovules.	No. of pollen bearing flowers.	No. of pollen grains.	Approximate ratio of ovules to pollen grains.
Dent Corn............	1520	9300	69750000	1 : 45000
Fint Corn............	940	6500	48750000	1 : 52000
Sweet Corn............	445	1560	11700000	1 : 26000

These figures would allow a range of from 25000 to 50000 pollen grains for each silk to be pollenated where there is only one ear on the plant. However, as Leavenby has pointed out, there is a great variation in the number of tassel flowers on different individuals in the same variety. There is also a difference in number of ears and from what we know now of differences in the size of anthers and the tassels on which they are borne, the differences in number of pollen grains must be much greater than in the cases selected by Lazenby. The fact that in some instances a large proportion of the pollen grains are infertile must also be recognized.

The first staminate flowers to mature are usually those in the upper part of the axis or central spike of the tassel the sequence being in both directions, but mostly downward and, on the branches, inward. When there is sunshine, more or less pollen is shed throughout the day, but the most of it falls during the forenoon. On days that are favorable, another, shorter period occurs in the evening, a short time before sunset. Either cold, wet weather or excessive heat may retard the process. Manipulation of the flower spike in the hand has an accelerating effect, probably due to friction and warmth of the hand, and a considerable quantity of viable pollen may be secured from mature flowers in this way.

The distance to which corn pollen is carried depends largely on the nature of the wind. A rising or whirling wind might readily carry pollen a much greater distance than a straight wind. Various limits have been placed upon the distance to which corn pollen is carried by the wind,—varying from 50 feet to a half mile. In our own work, we found the last blue kernel in a yellow variety at a distance of 20 rods (north) from our breeding plot which furnished the pollen for this kernel.

In breeding work with horticultural species, advantage has been taken of the fact that many kinds of pollen are viable for weeks and months. Booth 10) germinated grape pollen in New York, three weeks after it had been gathered in California. Sandsten 70) secured apple and plum pollen from Washington, Tennessee, Missouri, and Minnesota; testing it in Wisconsin he found that "a small percentage of apple pollen retained its vitality for six months, while but little plum pollen retained its germinating power this long." Supposedly authentic instances have been reported in which grape, tomato, and date pollen has remained viable two, six, and twelve months respectively 30).

Because of the difficulty experienced in getting very early and very late varieties of corn to bloom at the same time, it would be very desirable to store corn pollen or to be able to ship it over long distances, for hybridizing work. McCluer 57) reported that corn pollen seemed to retain its viability for several days if kept dry. Webber 85) stated that corn pollen retained its viability at least two weeks.

In our own work, more than a thousand tests were made on the viability of pollen and silks. The time in which they were retained ranged from 0 to 25 days in all the combinations made,—fresh pollen on old silks, old pollen on fresh silks, and the intermediate combinations. No reliable cases were found, including hybrids in all the groups and many varieties, in which shoots produced kernels when pollenated with pollen that had been stored 30 hours. Many successful cases were found in which the pollen was used in the morning and during the forenoon of the day after the one on which it was gathered. For satisfactory results it is best to use corn pollen on the same day on which it is gathered, discarding what is not used and getting a fresh supply on the morning of the next day in which pollenating work is to be done.

These conclusions are supported by the work of others, in which corn pollen was tested under different treatments and in various germinating solutions. Jost 47) states that corn pollen remained viable only one to two days under optimum conditions. Pfundt 68) found that pollen of corn remained viable only one day, alike in all the conditions under which it was kept.

There are many instances in plant species in which self-pollenation results in few or no viable seeds. Similar cases of sterility in hybrids are known. In an attempt at hybridizing two varieties of corn many years ago Gärtner reported securing only five kernels. Sturtevant 79) stated that "The agricultural species [sweet, flint, dent, soft, pop] have a strong tendency to resist cross fertilization with each other." Blaringhem 9) stated that many groups of corn do not hybridize among themselves but cited no authority in support of the statement. East 27) was unable to secure hybrids of Giant Missouri Cob Pipe, a large late dent corn, and Tom Thumb, an early dwarf pop variety.

On the other hand Kellerman and Swingle 48) concluded that "dent, flint, soft, sweet, and pop corn cross as freely with each other as with the different varieties in their own class." Collins 18) hybridized successfully the smallest Tom Thumb with large Guatemala and Mexican varieties. Emmerson 102) obtained a hybrid of Tom Thumb pop and a large, late dent corn.

As has previously been stated (see page 14) we are aware of no cases in our work in which widely diverse varieties such as are mentioned above would not hybridize when fresh silks and pollen are available.

In order to learn whether there are any differences in the external appearance of the pollen grains, pollen from a number of varieties was observed under the microscope. Fresh pollen was gathered and placed in the shade, part placed on glass slides, both covered and uncovered, and part of it being left in the bag;

in which it was gathered. It was found that the grains which were plump at first began to shrink immediately, giving it a deeper yellow color under the lens. In a number of samples, no plump grains were found after thirty minutes to an hour had elapsed and yet this shrunken pollen was viable when applied to silks. Ten pollen grains of from one to three representative plants, in various varieties taken at random, were measured and the empirical modes of the length-breadth measurements as well as the shape or outline of the pollen grains are given below:—

Size of freshly gathered pollen grains of various varieties (mm.).

Variety Number and Name			No. Pollen Grains Measured.	Breadth Mode.	Length Mode.	Shape Mode.
104.4–A	Pod Corn........	(medium sized kernels).......	30	.094	.146	elipse
104.4–B	Pod Corn.........	(medium sized kernels).......	30	.090	.098	pyriform
204.14	Yellow Rice Pop	(very small kernels...........	30	.078	.086	elipse
206.16	Red Pearl Pop...	(small kernels)................	30	.086	.098	pyriform
211.—	Yellow Pearl Pop	(Tom Thumbs—small kernels)	10	.090	094	elipse
212.22	White Rice Pop.	(very small kernels)..........	30	.078	.086	"
213.—	White Rice Pop.	(very small kernels)..........	30	.078	.086	"
304.—	White Flint	(very small plants—early)....	20	.086	.098	"
402.37	White Dent	(Hickory King—large kernels)	30	.082	.098	"
442.77	White Dent	(Cob pipe corn—med. kernels)	30	.086	.098	pyriform
504.—	Soft Corn	(medium kernels)............	30	.090	.098	elipse
612.92	Sweet Corn	(Egyptian—medium kernels)..	30	.090	.102	"

From these measurements it appears that there is no difference in size or shape of pollen grains which will interfere with their successful germination and subsequent fertilization of the ovules of any of the varieties used. The ratio between the modal length and breadth as shown in the above data bring out the fact that corn pollen is not exactly round as it has been reported by others. With regard to the inheritance of shape, normal long pollen grains have been reported to be dominant to round pollen grains in sweet peas 3). It was thought that difference similar to this might be found in corn pollen.

Correns 19) reported differences in receptivity to pollen when that of several varieties was applied to an ear at the same time. We have obtained similar results by using pollen from varieties of different colors and composition of kernels all on the same shoot and evidently there is a difference in germinating power or receptivity aside from mere viability of the pollen itself.

Difference in the shade of yellow in the fresh pollen of various varieties was found, some having light yellow and others darker yellow colors. Aside from this difference in color and perhaps in viability, we found nothing that would indicate distinguishable genetic differences in pollen grains of corn.

SHOOTS.

The immature female inflorencence of corn, composed of the undeveloped ear with its leafy involucre of bracts or "husks" upon a short stem or "shank", is commonly known as the "shoot". This name applies until the ovules have become fertilized and considerable enlargement of the young ear has taken place.

The theory concerning the differentiation of the inflorescence of corn into "tassel" and "ear", as has been mentioned previously, includes the idea that the shank or stalk of the ear-bearing branch has become shortened. This idea is substantiated by the frequent occurrence of very long shanks on individual plants in general field culture, the increase in length of shank being most frequent on the lower shoots. In the limited number of individuals of this nature observed in our work, the extremely long shanks were plainly due more to the increase in length of the internodes than to an increase in their number. Montgomery 59) stated that the number of nodes in the ear bearing branches coincided with the number of nodes found in the main culm above the point of attachment of the ear bearing branch, in a sweet corn plant which he studied.

From a number of counts we have made on several dent varieties, it appears that Montgomery's statement will not hold in some, and perhaps all, varieties. Only distinct internodes on the shanks were included in the counts and in the majority of cases there was a larger number of internodes on the shank than on the main culm above the point of attachment of the shoot; this is very evident where the ear is borne at the second or third node below the tassel. Incidentally it was noted that the number of these upper internodes on the culm was more constant in a variety than the number of shank internodes. If each husk on the shoot is counted and an internode assigned to all that are not paired or multiple, we would have many more internodes on the shoot than on the upper part of the culm (above the ear-bearing node). It is often difficult to get satisfactory counts on shank internodes because of telescoping near the ear. Certain varieties—notably pop corns—tend to produce secondary shoots on branches in the axils of the husks on the main ears; these secondary branches may have as many or more apparent internodes than are found on the main shank.

After four years of selection for erect and declining ears from a strain which had been previously cross-bred* for seven generations, Smith 76) reported; "that the ear branch or shank was on the average almost twice as long in the declining ear strain as in the erect-ear strain, the averages for that year being about twelve inches and seven inches respectively—the longer shanks had an average of a slightly larger number of internodes and correspondingly a larger number of husks."

In all the groups, individual plants may be found with very long shanks, but as yet we have no data upon their inheritance. Certain varieties tend to produce long shanks while others produce very short shanks but the character is a fluctuating one. The behavior of the $\times_1$ hybrids, in which flint, dent, sweet, and soft varieties with long shanks were used with other varieties having short shanks, indicate that long shanks are probably dominant to short shanks.

Barrenness.

"Barrenness", or failure to produce ears, differs from sterility in that the entire inflorescence may fail to develop, thus the fertility of the flower does not enter into consideration. Barrenness in corn may include failure to produce a tassel, as has already been stated, but the large majority of cases deal with the failure to produce normal shoots.

Detasseling has been resorted to in order to prevent the pollen from barren plants falling on the silks of individuals from which seed is to be saved for planting. Some uncertainty exists in this practice because of the difficulty of determining truly barren plants in some varieties at the time at which detasseling is done. Bull 11) reported that barren plants "may be discovered by the absence of the enlarged leaf sheath just above the joint where the ear should appear";

*Bred by individuals within the variety or strain.

while Soule and Vanatter 77) stated that they were unable to distinguish barren plants, at the time of tasseling, from those which develop late and eventually produce ears.

We are aware of no case of reported barrenness which has not been influenced largely by either environment or decreased vigor and it was at one time suggested that if barrenness is hereditary, the character would tend to eliminate itself 43, 45), but this was before it was generally known that characters detrimental or even fatal to the perpetuation of the species in the pure or homozygous state may yet be transmitted indefinitely by means of heterozygosis.

Plants upon which shoots develop extremely late are undesirable and such plants usually produce nubbins or poor ears and indicate weakness in general. It has been suggested that the best way to overcome this evil would be to discard the parent ears entirely and to select from such ear-rows in a breeding plot that produc vigorous shoots. Varieties differ very much in regard to size and development of shoots at tasseling and silking time, some varieties producing silks before the shoots leave the leaf sheaths while others develop large shoots before the silks appear. By delaying detasseling till just before the pollen begins to fall it is possible to differentiate between vigorous and weak plants in many varieties at least.

It sometimes happens that varieties producing some barren plants possess other characters which are desirable and since breeding blocks are generally limited in size the small amount of additional work necessary to detassel undesirable plants would be well worth while not only with regard to failure to produce good ears but also with regard to other undesirable features which are known to be transmitted to the progeny.

Since no case has yet been reported where the progeny of a hand-pollenated ear fertilized by the pollen of a barren plant have all been barren, it would seem that this behavior—provided it is hereditary—must be either a recessive or a composite character and be transmitted contrary to the behavior of sterile anthers mentioned on a preceeding page.

Husks.

The arrangement of husks about the ear varies within an individual shoot. They are most frequently two ranked and imbricate, but other arrangements are to be found, such as; paired, convolute, mixed arrangement, and multiple—not imbricate—arrangements, at husking time the outer ends or tips of the husks may be found on one side of the ear. This warping of the dead husks proceeds far enough in many cases to expose the ears on the opposite side.

In harvesting the crop in 1909, distinct differences were noted in the amount of husks about the ear and in 1910 a number of counts were made on different varieties and their X_1 generations. In securing these counts, all the husks on the shoot including those on the shank were taken. This was done at harvest time after full development had been attained.

A wide fluctuation in the varieties, in number of husks on the upper ear, was found. This wide fluctuation may be partially accounted for by the frequent prolifications of the inner husks. The number of parts in these prolifications is variable. Although extremes of six and twenty-eight husks were found, practically all the varieties overlapped in this character and variable results would therefore be expected in their progeny.

If it can be shown that the number of internodes on the shank are the same as the normal number of husks then it is evident that many of the husks are prolifications. Had it been possible to eliminate all proliferous husks and thus determine the number of primary ones (one to each internode) we would have expected more definite results.

If prolification is a recessive character in husks, as it appeared to be in the case of the ear mentioned on page 37, many of the contradictory cases in the $\times_1$ generations might be explained by this one fact alone. In some instances there may have been pairing of proliferous and non-proliferous character while in others, both parents may have had the proliferous character. The conclusion reached during the study of this character was that many normal husks are dominant to few normal husks.

General notes were taken on other characters of the husks. Thick and thin husks (without regard to number or width) were found to be varietal characters and in a number of $\times_1$ hybrids, thick husks were plainly dominant to thin husks. Thickness of the total layer or involucre, depends not only on the thickness of each husk and on the number of husks, but also on the width or degree of wrapping of the ear by each individual husk. In the $\times_1$ hybrids, the wide and well wrapped husks were dominant to the narrow type.

"The Central West desires a corn with loose shucks so as to be easily husked, while for protection against insects, the Southern States require a tightly fitting husk" 40). Market gardeners desire young ears well covered with husks which permit storing the roasting ears for a longer period than do the ears of those varieties poorly covered with husks. East 24) reports finding a row of sweet corn in an ear-row test of Stowell's Evergreen, in which the ears were especially well covered with husks and remained in table condition for over a week (presumably after picking) while ears from other rows remained in prime condition only one day.

On some varieties used in this study the husks were very loose even though the involucre was relatively thick, this was especially noticeable before the kernels on the ear had enlarged to any extent. The husks remained loose and creased throughout the season in some varieties while in others they were tightly stretched and forced to expand as the ear developed. This firm, compact, type of shoot was dominant to the loose type in the $\times_1$ hybrids and was very noticeable as the young ears were developing in the field.

The Mexican variety No. 408 produced shoots with many, wide, thick husks, the inner ones of which were folded or rugose longitudinally in the upper region and laterally rugose at the base. These rugose husks were constant in the 408 variety and dominant in its $\times_1$ hybrids. Collins 18) reports a hybrid in which the "inner husks were crumpled at the base of the ear, a not uncommon condition with thick husked varieties."

The absolute length or size of husks on the hybrids behaved much like the size of plants, being intermediate in some cases and in others equal to or greater than those of either of the parents. Varieties producing long ears necessarily develop long shoots and husks and length in these instances is dominant to shortness.

With regard to the relative length of the husks and ears or cobs, the behavior discloses an interesting difference. When hybrids were produced between a variety in which the mature husks extended beyond the tip of the ear and a variety in which ear and husks were conterminous, the hybrid invariably exhibited the latter character. But when either of these two types were hybridized with a type in which the ear protruded, the protruded ear character was dominant. All the plants of the pod variety No. 101 displayed the protruded ear character which was always dominant in its $\times_1$ hybrid progeny. One of the Mexican varieties (No. 410) produced approximately 50 per cent of individuals with protruded ears and this was a distinguishing character in its $\times_1$ hybrids. Collins 18) found a behavior similar to this in two cases in which a large number of the ears protruded beyond the husks in the $\times_1$ hybrids. In my results it appears that while long husks are a dominant character as well as the long ear, the long ear yet exceeds the long husks in relative as well as absolute length.

The husks of most varieties are green but in some a red tinge is frequent. This red tinge, which is often associated with red tinge on the culm, appeared in the X_1 generation from parents having green husks hybridized with other parents having red tinge husks. Red husked plants were frequent in the variety No. 408 as well as in the hybrids in which it was one of the parents, and homozygote red husks would be expected to be dominant to red tinge and pure green husks.

Laminae.

Many years ago, Goethe, the great German naturalist-poet, announced the theory that floral parts are nothing more than modified leaves. This idea is perhaps no more beautifully illustrated than in the enveloping involucre or husks of an ear of corn. When the shank in the shoot is relatively long the lower husks assume the form of true leaves. With a tendency toward a shorter shank, there is a decrease in the leaf-blade until the leaf sheath, which has become a husk, bears a very small blade or none at all.

In some varieties these small leaf blades or "laminae" persist on the outer husks and in some individuals (occurring in all the species groups) these laminae may equal the length of leaves—two feet or more in length in extreme cases. Development of unusually long laminae is generally associated with long shanks and small ears. In those in which extremely broad laminae were developed, the size of the ear was also generally diminished.

As a varietal character, long laminae are more often found in the flint, sweet, and soft groups. Varieties producing very short or no laminae are more often found in the dent and pop groups.

In studying the behavior of length of laminae, we are dealing again with a fluctuating character and one which, similar to the suckering character, seems not entirely lost in any variety. In addition to this fluctuation between plants in the parent strains, there is also another and similar fluctuation upon the individual plant. The laminae on the lower shoots are nearly always longer than the laminae on the upper shoot, and a similar increase in length exists on a single shoot from the tip downward.

Because of this variation in length of laminae, it was found impracticable to secure exact measurement and the data were taken with respect to the length of laminae on the upper shoot only and as compared to the relative length of the shoot on which they were borne. While this method was only an approximate one, the data were all secured by the same person and, aside from a possible bias in judgment, the classification was uniformly made in all the parent varieties and X_1 progeny.

It was noticed that few of the varieties are constant to the "Type Group" in which they fall and distinct genetic differences within a variety, and consequently variable results in the hybrids, are to be expected. Seven of the ten hybrid cases which gave an "Average" result were such in which the parents had like modes and the hybrids produced the same. Eliminating these seven cases, the large number of the hybrid results would appear to fall at either extreme as shown in the summary. This should not occur if there is a genetic difference in length of laminae.

Among the remaining 29 cases on which data were taken, a small majority indicate dominance of the long laminae. Certain hybrids displayed this dominance of long laminae so markedly that we would expect this result in all cases where homozygous parents are used. The mixture in varieties is evidenced by the results secured in the closes in which there were distinct differences in behavior while all the X_1 results would have been expected to fall in the "average" list. The selfed cases as usual are limited in number but indicate a decrease in the length of laminae.

Occasional individuals occur having abnormally broad laminae, the inheritance of which has not been determined. One variety (No. 214B) frequently having short, broad laminae gave, in its hybrid with a variety (No. 210) having short narrow laminae, medium and broad laminae.

The colors of the laminae are generally the same as those of the leaves on the plant and behave similarly in transmission.

Silks.

The most conspicuous phenomenon in connection with the development of the shoot is the appearance of the silks. Their growth is very rapid and their period of usefulness limited. When pollenation of these silks or "styles" is prevented they may continue to grow for a number of days. Lazenby 52) reported that "Some of the silks [of a dent variety] attained a total length of over eighteen inches."

In our study of the receptivity of silks of various ages, a number of individuals were found which had attained a length of 8 to 14 inches beyond the tip of the shoot. This behavior might be considered as an adaptation to provide a fresh surface upon which the pollen may lodge, but the length to which the silks may grow is apparently correlated with the length of the cob from which they arise.

As has been reported under "Technic", the silks are receptive at any point and clipping them back does not interfere with the subsequent fertilization of the ovules by pollen applied after the silks have been clipped. This test was also applied by Kellerman and Swingle 48), and in addition they opened the husks of some shoots before the silks appeared and succeeded in getting poorly filled ears by applying pollen in this way. From our own observations in repeating this experiment, it was found that only those silks were receptive which would have appeared very soon after the time at which the husks were opened. When the husks were stripped back on the shoots which had silks well exposed, and pollen applied to the portion of the silks within the shoot, successful fertilization was effected.

The silks, which are double in structure, are more or less hairy near the extremity and an erroneous idea has been given in popular descriptions of the process of fertilization of the silks, by the statement that these hairs catch and hold the pollen in their grasp. The hairs provide an increased surface upon which the pollen may lodge, but the moist surfaces of the silks and pollen grains alone serve to hold the grains which must germinate very quickly judging from the very short period in which corn pollen is viable when exposed in a normal atmosphere.

Some writers state that the silks from the base of the ear appear first and the ovules from which they come are consequently fertilized before the others on the ear 11). This statement is true only in the broad sense—meaning the lower portion of the ear. Among the many ears secured in our work by hand pollenating silks of various ages, we found many imperfectly filled butts and bare tips on ears which were pollenated soon after the first silks appeared.

The double pollenated ear—No. 2S3.170—was an instance of this nature. The dam of this particular ear was a white pearl pop (No. 210). On the first day on which the silks appeared, it was pollenated from its own tassel (selfed). Six days later, pollen was applied from a variety having a yellow endosperm (No. 309). As has been stated, the selfed and hybrid kernels were determined by the differnce in color and a distinct band of pure white kernels was found at some distance above the butt of the ear. The remainder of the kernels below and above this band were yellow. A number of other and similar cases were found.

At the end of the six days, the silks at the tip of this particular ear had not yet developed for the reception of pollen as was shown by the bare cob at this point. This regularity of distribution does not appear on all ears, many of which have irregular patches of kernels evidently due to the uneven development of silks

on various parts of the spike. From the many hand-pollenated ears secured, the longest interval of time between the first apeparance of-silks and the last date on which the younger silks on the same ear were yet receptive was thirteen days, and in this case only a few kernels at the tip of the cob were secured. Entire ears may be pollenated fully in the natural way in a period ranging from two to ten days, depending upon the variety and conditions.

Differences in the size and structure of silks were found but no attempt was made to study their behavior in the hybrids. In varieties having colored silks (other than pure green or yellowish green) the hairs on the silks are the first and frequently the only parts to become colored.

No variety was found which was homozygote to silk color but the populations from selfed seed showed exact uniformity in color of silks in most of the cases. In one of these $\times_1$ selfed cases (No. 201$\times$S) silks were produced having a dark yellowish-green color; the behavior of this color on hybridization has not been determined. Several cases were found in which dark green silks were dominant to light green silks in the $\times_1$ generation. Green silks $\times$ green silks in most cases gave green silks only, but several cases were found in which only parents with green silks had been used, where the $\times_1$ generation showed some individuals with red tinge or reddish green silks. Without a knowledge of the ancestry previous to 1909, we are unable to state whether such cases are due to heterozygosis which did not shown in 1909 or whether they are due to new combinations in the $\times$ generation.

The notes on the silks were taken somewhat early in their development in many cases and it is possible that some of the parents developed a red color after the notes were taken. In general the order of dominance of silk color appears to be as follows: dark red, reddish green, red tinge, to green. Numerous cases have been reported by others in which the deep red silk appears to be dominant to the green and red tinge silk.

The behavior of the various shades of green fall in a separate category from that of the reds, and either of the greens may be obscured by the red color. It is very doubtful whether red tinges which are absolutely constant to degree of coloration can be secured.

Position of the Upper Shoot

Instances have been reported which permit the general conclusion that shoots may be produced in the axil of any leaf on the culm or its branches. Among the varieties used in this investigation we found ears at various heights on plants and at all internodes below the tassel, while small ears at the base of the tassel are not uncommon, but a rather definite location for the production of the main ear-bearing shoot exists in the different varieties. The number of upper internodes (between the tassel and the upper or main ear-bearing shoot) is more constant throughout the varieties of corn, than is the number of lower internodes (below the upper shoot).

The results secured at the Illinois Experiment Station 76) in selecting for "high" and "low" ears, gives evidence in support of the above statement. Height of ear in inches above the soil was made the basis of selection in this instance. Data were also secured upon the total height of the plant, number of internodes below the ear, and the total number of internodes on the plant. If from this data we compare the difference between the number of internodes below the ear and the total number on the plant, we find that this difference (7 internodes) was always the same in both plots except in one year. In this aberrant year, the "high-ear" difference was six internodes and the "low-ear" difference only five internodes. The cause of this is not known, but it is important to note that the exceptions occurred on both plots in the same year. If the deviation of one were added

to the total number of internodes givēn for the "high-ear" plot and the deviation of two to the number given for the "low-ear" plot in that year, it would at least make the "total internode" columns for the six years more uniform as well as to give *exact uniformity* in the number of upper internodes in both plots for all the years.

From the data, it is also evident that there has been no change in the "high-ear" plot in the height of ear, neither in inches nor in number of internodes. Neither is there any change evident in this plot in regard to total height of plant and total number of internodes. The difference (three feet), which now exists between the two plots is due solely to a change in the "low-ear" plot in which the height of ear, both in inches and number of internodes, is but little greater than half of what it was at the beginning. There has also, apparently, been no change in length above the ear in the low ear selections; the average length in inches above the ear being slightly more in the low-ear plot than in the high-ear plot.

This decrease, which has been found in the "low-ear" strain, suggests the idea that homozygous "low-ears" have been selected and mated from within a heterozygous population. The fact that the "High-ear" strain has remained constant with only slight fluctuations, readily attributable to seasonal differences, suggests in a similar way that the parents of this strain were either homozygous "High-ears", or that this is the dominant character and that extracted "High-ears" have been selected, thus maintaining but not materially increasing the height of the strain. As in the case of the differences in oil and protein secured in other strains, no one can say positively as yet what is happening in these experiments of far-reaching importance.

Data were taken to secure exact information upon the behavior of the relative height of the upper shoot. It is significant that there is a very close uniformity between all the parent varieties in the number of upper internodes (above the upper shoot), irrespective of the number of lower internodes. It is also significant in comparing cases, that this internodal height of the upper shoot or ear is not affected by the number of shoots on the culm.

As was stated previously; it is difficult to determine the internodes at the base of the plant at the time of maturity, and it is evident that a shortening of internodes at this point is partially the cause of fluctuation in the number of lower internodes, apparent at maturity, in some varieties.

The reciprocals indicated small differences but in general these cases are fairly uniform.

The summary of the data shows that a large majority of the hybrids are above the average of the parents in number of lower internodes. The results in the closes and selfs indicate that individual parents were used which had a greater number of lower internodes than the mode of the variety from which they came; a result contrary to that which would be expected from inbred progeny.

The summary of results with respect to the number of upper internodes is indefinite and had the study of relative height of the upper shoot been made only with respect to its distance from the tassel, no definite conclusions would have been reached. The extremes in the number of upper internodes in all the parent modes are five and eight, which, with the existing fluctuations, allows the parent arrays to overlap and does not provide sufficient difference for marked differentation in the $\times_1$ hybrids. The fact that the majority of the fourteen hybrids fall in the average group is attributable to the use of parents which were very similar in this respect. No definite concluiosns can be made on the behavior of the $\times_1$ closes and selfs.

In order to check the behavior of the upper and lower internodes simultaneously on the same population, the "Relative Height on the Plant" was computed from the sum of the two modes. In the data secured in this way, we find that in the large majority of cases the relative height of the upper shoot in the $\times_1$ hybrids

is equal to or greater than that of either of the parent modes, therefore, relatively high ears on the corn plant must be a dominant character.

Number of Shoots.

Perhaps no organ of the corn plant is more dependent upon environment and vigor of growth than the shoot containing the undeveloped ear. While certain varieties normally produce a large number of shoots in comparison to other varieties, adverse conditions may inhibit their development entirely.

While the large majority of shoots on the lower part of the stem may fail to produce ears, their partial development is an indication of an ear bearing tendency, and as such is important in a study of characters in the corn plant. How the difference among varieties in shooting tendency and prolificacy in ear production came to exist, is not known, but it is evident that there must be a close correlation between this and other characters in the plant. As an example, the production of an extremely large ear in the upper shoot is not associated with a large number of ears, and those varieties producing a large number of shoots generally have small ears.

It is evident that the production of shoots is closely related to the production of suckers, and individual plants are frequently found in which it is difficult to distinguish between the lower shoots and the suckers. Card 12) made selections in a variety of sweet corn for large number of ears on the plant, and found that the increase which he secured came chiefly from the increase in the number of ear-bearing suckers.

My data was obtained by counting all the shoots which extended beyond the leaf-sheaths on the main culm of each plant. This data, therefore, includes a very large proportion of shoots within which ears failed to develop. Data were also secured upon the number of ears harvested and, as would be expected, those varieties producing a large number of shoots also tended to produce a large number of ears. The same parents and hybrids used in the study of behavior of number of internodes were used in this instance, and it is evident that with a given number of internodes sufficient to permit the development of numerous shoots, the number of shoots actually developing does not appear to have any relation to the relative height at which they are borne.

As usual, interesting differences in behavior were found when one parent variety was used in different combinations with other varieties. The reciprocals in this table gave quite uniform results as is shown by the arrays in each case.

The summary of the $\times_1$ hybrids places the large majority above the average of the parents in the production of shoots. As has been noted, the production of shoots depends to a large extent upon vigor of growth and therefore hybridization should favor the development of a large number of shoots. Leaving out the 11 cases which gave a number of internodes above those of the greater parent, which result might be attributed to increased vigor, the remaining hybrids in the summary yet show that a "large number of shoots" on the main culm is dominant to a "small number of shoots".

Close pollenation in the majority of cases evidently had no limiting effect upon the development of shoots in this one season. Among the selfed cases only two showed a decided decrease in the production of shoots, while one (310$\times$S) of the six cases produced a mode slightly above that of the parent mode of the previous year. A comparison of all the parent modes in both years shows that the modes for 1910 were generally higher than those in 1909; therefore, the selfed case, having an apaprent slight increase, must have been the result of difference in seasons.

As is the case with all the other characters discussed in this paper we must consider not only environmental influences but the probable genetic differences

within the populations studied. The important fact brought out by the summaries of the various tables is: that in order to get definite results we must have individuals pure with respect to the character with which we are concerned, or at least observe their behavior in the second controlled generation when the data carefully secured may be just as reliable, regardless of the mixture in the original parents.

APPENDIX

The writer, Walter Byron Gernert, graduated from the Kansas State Agricultural College in June 1907 with the degree of Bachelor of Science in Agriculture. In September 1907 he entered the Graduate School of the University of Illinois, from which he received the degree of Master of Science in Agronomy in 1909.

During the years 1905-'07 he was Student Assistant in the Kansas Experiment Station and was later connected with the Illinois State Soil Survey through the field seasons of 1907 and 1908. He held a Fellowship in Agronomy in the University of Illinois during the academic years 1908-'11.

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